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FURTHER POLLEN STUDIES OF POST PLEISTOCENE BOGS IN THE PUGET LOWLAND OF WASHINGTON[1]

HENRY P. HANSEN

(WITH TWO FIGURES)

INTRODUCTION

The modification of the topography by Pleistocene glaciation and the humid climate in the Puget Sound basin of western Washington has been favorable for the development of a larger number of bogs than in other areas of the Pacific northwest. The peat deposits are representatively located, and because the entire region is more or less homogeneous in topography, soil, climate, and phytogeography, pollen analyses of well-distributed bogs should reconstruct a fairly accurate picture of postglacial forest succession and general climatic trends. This study is concerned with further pollen analyses of peat deposits located within this physiographic province. Four other deposits, two in southwestern British Columbia and two near Seattle, have been previously studied, and all six pollen profiles seem to agree essentially on the indicated postglacial forest succession (Hansen 1938, 1940a). This region was glaciated by both the Admiralty and the Vashon glaciers of the Pleistocene (Bretz 1913), and the latter has been generally correlated chronologically with the Wisconsin glaciation of the middle west (Antevs 1929). Fenneman (1931) classifies this region as the Puget Trough of the Pacific Border Province.

The first bog is located a few miles north of Black Diamond, King County, in sect. 35 of T. 22 N., R. 6 E., approximately 20 miles east of Puget Sound, and at an elevation of about 450 feet above sea level. The depression in which it has been developed apparently was formed in irregular ground moraine or by damming of a small preglacial stream valley. The surrounding terrain is irregular and covered with glacial drift but is not extremely rugged. The bog is surrounded by a marginal ditch that supports a dense growth of willow (*Salix Scouleriana*) and hardhack (*Spiraea Douglasii*). Near the northern margin a shallow, intermittent pond persists wherein grow yellow pondlily (*Nymphozanthus polysepala*), buckbean (*Menyanthes trifoliata*),

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and *Dulichium arundinaceum*. The central and larger area is covered chiefly with Labrador tea (*Ledum groenlandicum*), bog laurel (*Kalmia polifolia*), cotton grass (*Eriophorum gracile*), buckbean, sedge (*Carex* spp.), *Sphagnum* sp., and *Polytrichum juniperinum*. An extensive zone of hardhack surrounds this community and is gradually encroaching upon it. An invasion by lodgepole pine (*Pinus contorta*) was under way, but has been destroyed by fire. On higher ground adjacent to the bog grow red alder (*Alnus rubra*), largeleaf maple (*Acer macrophyllum*), vine maple (*A. circinatum*), ocean spray (*Holodiscus discolor*), syringa (*Philadelphus Gordonianus*), Oregon ash (*Fraxinus oregana*), elderberry (*Sambucus callicarpa*), blueberry (*Vaccinium ovatum*), salal (*Gaultheria shallon*), dewberry (*Rubus macropetalus*), fireweed (*Epilobium angustifolium*), bracken fern (*Pteridium aquilinum*), and Douglas fir (*Pseudotsuga taxifolia*). Many other herbaceous plants also exist in this community.

Peat samples were obtained with a Hiller borer at quarter-meter intervals. The depth of the bog approximately in the center is 6 meters and it is underlain with sand. There are greater depths indicated by a profile taken by Rigg and Richardson (1938). The lower quarter meter consists of silt, followed by limnic peat grading at 4 meters into fibrous peat which is present to the surface. Volcanic ash crystals occur at the 2-meter level, while in other parts of the bog ash exists as a well-defined layer. Ash is present in most of the bogs in the Pacific northwest, and may occur as a layer or dispersed crystals, which is apparently determined by the stage of hydrarch succession at the time of eruption. *Sphagnum* leaves first appear at 3.5 meters.

The other bog is located about 3 miles north of Sedro Woolley, Skagit County, in sect. 31 of T. 36 N., R. 5 E. It lies about 12 miles east of Puget Sound and almost 100 miles north of the former bog. The depression in which it has been formed had its origin as a kettle pond in terraced outwash of the Samish River. The elevation is about 350 feet above sea level, and the foothills of the Cascade Range rise immediately to the east. The bog comprises about 80 acres, with a deep lake persisting in the center. A submerged hydrosere exists in the lake, with a floating hydrosere of pondweed (*Potamogeton natans*) and yellow pondlily near the shore. Along the shore grow clumps of cattail (*Typha latifolia*), purple marshlocks (*Potentilla palustris*), sedge, and *Sphagnum*. Farther inland thrive Labrador tea, bog laurel, cranberry (*Vaccinium oxycoccus*), and hardhack. On the margin of the bog are alder, willow, and other shrubby plants similar to those around the other. The southern portion is annually mowed for hay, while on the northern margin it is being sparingly invaded by trees, including western hemlock (*Tsuga heterophylla*), western white pine (*Pinus monticola*), and lodgepole pine. Peat samples were obtained with a Hiller borer at quarter-meter intervals about 50 feet south of the lake. Here the lacustrine deposits are 9.5 meters

deep, the lower two and one-quarter meters composed of blue clay with a distinct metallic sheen. This was probably carried into the lake in late glacial or early postglacial time before the invasion of forests, as it is entirely devoid of pollen. The clay changes into dark limnic peat at 7.25 meters, which in turn grades into brown fibrous peat at 4 meters; the latter is present to the surface. *Sphagnum* leaves first appear at 6.5 meters. No volcanic ash was found, either as a layer or dispersed crystals.

FORESTS IN ADJACENT AREAS

Since both bogs lie within the same physiographic, climatic, and phytogeographic province, a discussion of the general phytosociological aspects may be applied to areas in the vicinity of both. All of the Puget lowland in western Washington lies within the Humid Transition life zone (Piper 1906). The most characteristic tree of this zone is Douglas fir, and before lumbering, fire, and cultivation removed the virgin forest it was the predominant tree in most areas. Clements' classification of the major vegetation climaxes of North America includes the Puget Sound lowland in the hemlock-cedar association of the Coast Forest (Weaver and Clements 1938). In this formation western hemlock, western red cedar (*Thuja plicata*) and Douglas fir are the chief dominants, the latter persisting as a subclimax species because of its aggressiveness in invading areas denuded by fire. However, the seedlings of Douglas fir do not grow on the forest floor, while the more tolerant hemlock, cedar, and lowland white fir (*Abies grandis*) readily gain a foothold and form an understory. The stand of Douglas fir gradually thins out because of wind, insects, disease, and lack of reproduction, whereas the others continue to expand. Eventually, if fire and lumbering do not disrupt normal forest succession, hemlock, cedar, and lowland white fir will form the climax forest with large and mature Douglas fir scattered throughout. Munger (1940), studying the composition of forests of various ages, has shown that without fire or logging a Douglas fir forest would probably be converted to the climax type in five or six centuries. Other conifers of lesser importance in the Humid Transition zone include western white pine, lodgepole pine, Sitka spruce (*Picea sitchensis*), and silver fir (*Abies amabilis*). Western white pine occurs occasionally on open knolls and well drained areas where the climax forest has been removed, and lodgepole pine is often the pioneer invader of bogs or areas where the soil has been disturbed. Sitka spruce is not common but may be locally abundant on swampy floodplains near sea level, while silver fir grows mixed with other conifers at higher elevations. Broadleaf trees and shrubs consist chiefly of red alder, broadleaf maple, Oregon ash, cottonwood (*Populus trichocarpa*), several species of willow, and many other species of shrubs. These plants occur abundantly on favorable sites as members of associes, facies, and socies. The western boun-

dary of the Canadian zone occupying higher altitudes lies about 20 miles to the east of both bogs.

Forest type maps (1936) indicate 12 forest types within a distance of 8 miles from each bog. Douglas fir types of several size-classes constitute about 75 per cent of the forest cover in the vicinity of the Black Diamond bog. Other types in order of the size of their area are agricultural and non-agricultural lands, recent and non-restocked cutovers, hardwoods, and spruce-hemlock-cedar. Adjacent to the Sedro Woolley bog recent and non-restocked cutovers comprise about 25 per cent of the area, and Douglas fir types of all size-classes comprise an equal area. Other types in order of their area include non-agricultural lands, spruce-hemlock-cedar, hardwoods, and a small area of balsam fir–mountain hemlock–upper slope type. The latter type does not exist within 8 miles of the Black Diamond bog. The spruce-hemlock-cedar type is more extensive and nearer to the Sedro Woolley bog, and is better represented by higher proportions of western hemlock and Sitka spruce pollen in the upper levels. On the other hand, Douglas fir is recorded in a much greater proportion in the upper levels of the Black Diamond bog, because of the large area occupied by Douglas fir types in this vicinity. It is probable that pollen from forests well beyond an 8 mile radius is recorded, but the relative area covered by different forest types adjacent to peat deposits seem to be somewhat proportionately reflected in the upper strata (Hansen 1940b).

In his classification of the climatic provinces of North America, Thornthwaite (1931) designates most of the Puget Sound basin as having a humid, microthermal climate with adequate precipitation at all seasons. Thornthwaite's climatic provinces are based upon the relation between humidity, temperature, and seasonal distribution of precipitation. A small area adjoining the southeastern tip of Puget Sound is indicated as having a similar climate, but with a summer deficiency in precipitation. This area is spoken of locally as the "Tacoma prairies" (Jones 1936), because of the general absence of forests, although at present it is being invaded by oak (*Quercus Garryana*) and Douglas fir. It is possible, however, that the porosity of the gravelly glacial outwash that covers this area and its rapid drainage are more responsible for the dearth of trees than the limited summer rainfall. The mean annual precipitation at Tacoma, Washington, is greater than in other Puget Sound areas that support the hemlock-cedar climax forest. Piper (1906) designated this area as the Humid Transition (prairies) life zone. The mean annual precipitation at Kent, about 10 miles west of the Black Diamond bog is approximately 37 inches, and at Sedro Woolley 47 inches (U. S. Weather Bureau 1936). A higher proportion of the annual precipitation occurs during the growing months at the latter station. The rainfall at Kent, however, is somewhat lower than at higher elevations to the

TABLE 1

Percentages of fossil pollen, Black Diamond Bog.

Depth in meters:	6.0	5.75	5.5	5.25	5.0	4.75	4.5	4.25	4.0	3.75	3.5	3.25	3.0	2.75	2.5	2.25	2.0	1.75	1.5	1.25	1.0	0.75	0.50	0.25	0.0
Pinus contorta	74	70	76	70	70	26	24	30	20	16	15	10	12	8	16	2	3		4	1	2	1	4	10	4
P. monticola	18	21	13	15	12	4	2	6	4	5	6	7	8	14	8	8	6	8	8	4	4	1	1	5	2
Pseudotsuga taxifolia	1	1	1	5	10	50	58	52	61	63	62	62	60	54	52	62	60	45	50	43	47	46	37	36	33
Tsuga heterophylla	1	2	2	2	4	10	4	4	8	8	8	12	11	16	17	20	22	40	33	47	40	45	45	42	54
Picea sitchensis	5	4	6	4	1	2	4	4	3	4	5	4	4	4	1	2	1	1	1	2	1	3	2	4	1
Abies grandis	1	2	2	4	3	8	8	4	4	4	4	5	5	4	6	6	8	6	4	3	6	4	11	3	6
Pinus spp.[1]	10	16	19	22	17	11	9	13	7	3	5	7	7	11	12	6	3	2	5	1	3	3			1
Gramineae[2]			1		1			2	1	1		1	4		2	1	1		1						
Compositae[2]		2			2						1						1							1	
Chenopod-Amaranth[2]	1								1													2			
Alnus[2]	18	21	14	19	17	15	13	26	25	22	97	37	110	29	72	35	78	25	30	53	44	31	57	37	64
Acer[2]	1	3	2	6	5	1	1		7	2	14		2	6			3	1	6	2	1	7	1	3	8
Betula[2]											3	1	2	1	1		10	12	6	5	4	4		2	
Salix[2]	1			3	1		1			3	1	67	36	33	27	12	3		7	1	2	1		2	7
Ericaceae[2]							1							1			5	1	1		1	2	9	62	8
Cyperaceae[2]	3	2	1	7	1	1	2	7	3	7	5	12	6		3	13	19	10	6	20	17	3	2	3	6
Nymphozanthus[2]					3		2	4	3	3	1	1	3		9	2	4	3	3			4	15		
Typha[2]								2	1	1			1			1									

[1] Number of pine pollen grains discarded as unknown, not computed in the percentages.

[2] Number of grains not computed in the percentages.

east in the vicinity of the Black Diamond bog. Greater rainfall occurs at Sedro Woolley because of its location opposite the Straits of Juan de Fuca, while areas farther south in the Puget lowland are protected by the Olympic Mountains.

METHODS

In preparation for study about 2 cc. of peat were boiled in a weak solution of potassium hydrate, strained through cheesecloth, washed, centrifuged, stained with gentian violet, and mounted in glycerin jelly. Exactly 150 significant pollen grains were identified from each level. The non-significant pollen was also recorded but not used in the computation of percentages (tables 1, 2). Non-significant pollen is that from plants growing locally on or near the bog, and is probably not indicative of adjacent forest succession. The significant species recorded as less than 1.5 per cent at any level are listed in the tables as 1 per cent.

The identification of the species of *Pinus* and *Abies* pollen was based on their size ranges as described in a previous paper (Hansen 1940b). For previous papers, as for this, 200 pollen grains of each Pacific northwest species of *Abies*, *Pinus*, and *Picea* were measured and their size ranges determined. The modern pollen was fossilized with a weak solution of potassium hydrate and mounted in glycerin jelly to simulate the conditions employed in preparing peat slides. All modern pollen was taken from living trees when mature and being shed, rather than from herbarium specimens. In using pollen from dried herbarium specimens there may be danger that the pollen was not fully mature, and had not attained its full size when collected. On the other hand, if the pollen were mature, there is the possibility that most of the pollen had been shed and that the remainder is not normal in size or shape. The latter situation is more significant when the size-variation frequency curve is used in the form of histograms for comparison with the size-variation frequency of fossil pollen. A dearth of pollen of average size was noted by the author for *Pinus contorta*, *P. ponderosa*, and *P. albicaulis* taken from dried specimens and immature fresh specimens, which will be discussed in a later paper on size-variation frequency of Pacific northwest conifer pollens.

In order of their size beginning with the smallest are *Pinus contorta*, *P. monticola*, *P. albicaulis*, and *P. ponderosa;* the firs are *Abies lasiocarpa*, *A. grandis*, *A. amabilis*, and *A. nobilis;* and the spruces are *Picea sitchensis* and *P. Engelmanni*. The size range of each species overlaps that of both smaller and larger species, with the exception of lodgepole pine which seems to overlap western white pine slightly or not at all. *Pinus albicaulis* overlaps white and yellow pine, which makes it impractical to attempt to separate this species from the other two. White-bark pine, however, is a timberline tree

TABLE 2

Percentages of fossil pollen, Sedro Woolley Bog.

Depth in meters:	7.25	7.0	6.75	6.5	6.25	6.0	5.75	5.5	5.25	5.0	4.75	4.5	4.25	4.0	3.75	3.5	3.25	3.0	2.75	2.5	2.25	2.0	1.75	1.5	1.25	1.0	0.75	0.5	0.25	0.0
Pinus contorta	66	48	32	33	14	24	8	10	7	8	2	5	8	6	1	5	3	6		3		1	2	2	1	2	1	1	1	3
P. monticola	16	12	7	5	6	2	5	1	2	3	2	1	3	2	2	3	8	2	2	3	3	4	3	2	1	5	8	6	4	10
Pseudotsuga taxifolia	5	14	36	46	62	61	60	66	66	61	64	60	48	53	49	40	45	44	35	30	31	30	18	22	28	23	25	26	31	10
Tsuga heterophylla	1	8	6	8	10	8	15	12	8	12	18	19	27	23	30	33	27	34	47	55	56	53	57	60	50	50	50	51	48	61
Picea sitchensis	10	4	3	3	4	1	2	1	1	1	4	3	4	2	4	2	2	2	6	3	6	6	17	8	16	12	14	14	13	7
Abies grandis	2	13	16	5	4	4	10	10	16	15	10	12	10	14	14	17	15	12	10	6	4	6	3	6	4	8	2	2	3	8
Pinus spp.[1]	16	6	3	8	2	5	2	1	1	3		2	4	4		1	7	4	1		3	1	4	1		7	9	6	3	8
Gramineae[2]									1				2	1	1						5		1			1		1	3	5
Compositae[2]				1														1											2	3
Alnus[2]	23	41	20	46	16	21	15	31	10	55	15	22	6	15	33	37	26	47	20	60	27	33	52	11	30	17	41	57	12	78
Acer[2]	1	3	1	2		1	1	1		1	2		3	1	7	2			7	1		2	6				3			2
Betula[2]								1					1		1		1		1		1	1						2	1	1
Salix[2]	3	1	2			5					7		5	10	2	3	6	3	11	8	9	17	12	1			8	11	2	3
Fraxinus[2]											1																			
Ericaceae[2]		1							1					1	1								1			1		4	1	2
Cyperaceae[2]	2	6	3	2	3	1		6	2	6	2	5	3	8	1		2	4	7	11	6	5	6	23	31		7	8	26	11
Nymphozanthus[2]	1	8	6	12	14	6	3	10	2	5	7	8	1	1	1	1			3	6	5	3	6	5	5	1	7	10	6	2
Typha[2]	1	1	6	3	3		1	4	5	5	1	3	5	1	2		12	2	5	3	4		2	2	3		4	2		1

[1] Number of pine pollen grains discarded as unknown, not computed in the percentages.
[2] Number of grains not computed in the percentages.

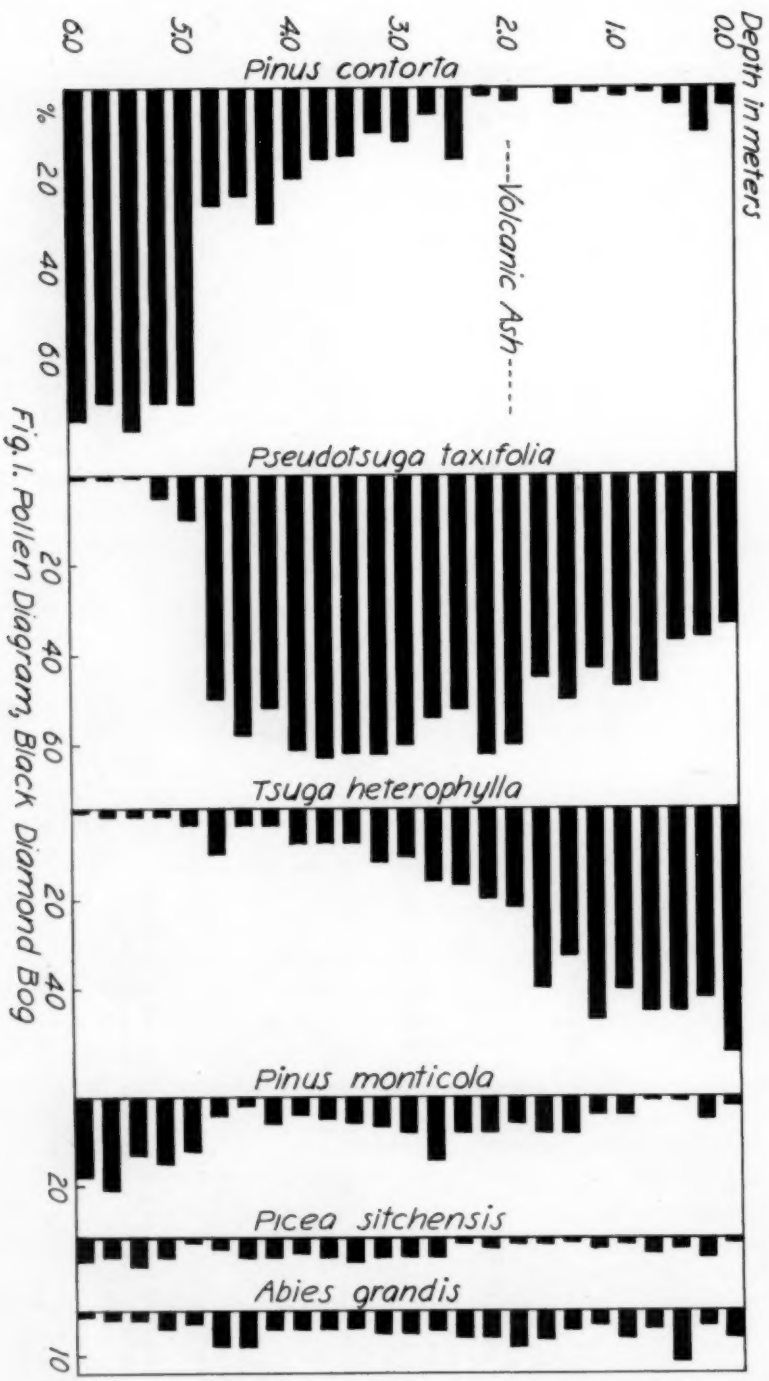

Fig. 1. Pollen Diagram, Black Diamond Bog

and probably never was abundant during postglacial forest succession. Likewise *Abies amabilis* overlaps the smaller *A. grandis* and larger *A. nobilis* and is virtually impossible to separate from these two species. No attempt has been made in this paper to separate silver fir, although all of the fir pollen falls within the range of lowland white fir. Whereas the pollen size ranges of Sitka and Engelmann spruce overlap to some extent, their geographic ranges are not known to overlap in Washington. In this paper it is assumed that all spruce pollen is that of Sitka spruce, because of the low altitude of the bogs and adjacent areas. It is realized, however, that Engelmann spruce pollen may have reached the bogs from higher altitudes to the east. An interesting and important fact was learned recently concerning the pollen of mountain hemlock (*Tsuga Mertensiana*). Pollen of this species collected on Mt. Rainier was found to have bladders, somewhat similar to that of pine, fir, and spruce. It may be differentiated from these species, however, because of the spheroidal cell and fine reticulum of the bladders. Through correspondence with Wodehouse after his examination of the pollen it was found that he had learned of the bladders on mountain hemlock after he had published his book on pollen (1935). He refers to the presence of bladders on fossil hemlock pollen from the Eocene and Tertiary, some with and some without, and all gradations between. Pollen collected from presumably *Tsuga Mertensiana* on the University of Washington campus at Seattle has no bladders, which may indicate a similar gradation for this species. A further check, however, as well as collection of pollen from other trees must be made to verify or refute this possibility. The pollen of *Thuja plicata* seems to be indistinguishable from that of species of *Chamaecyparis, Juniperus*, and *Taxus*. Pollen of western red cedar and other similar genera is not well preserved in peat deposits, although cedar is one of the chief dominants in the coast forest. This is evidenced by the apparent absence of cedar pollen in the upper strata of peat deposits even though this tree may live on the bog itself. Observations suggest that western red cedar does not produce as much pollen as pine, Douglas fir, and hemlock, which adds to its degree of under-representation. Pollen profiles are therefore somewhat distorted, especially in the upper levels, since red cedar probably has played no small part in later postglacial forest succession.

In identifying fossil pollen the size of the cell is noted and if within the limits of overlap of other species of the same genus, distorted in shape, broken, or impossible to measure because of its position, it is discarded as an unknown. In previous papers the proportion of conifer pollen thus discarded varied from less than 1 to 12 per cent of the rest of the significant pollen. In this paper the number of discarded pine pollen grains for each level is listed in the tables. The separation of species of pine pollen is not so difficult nor so important in the Puget lowland as in montane bogs east of

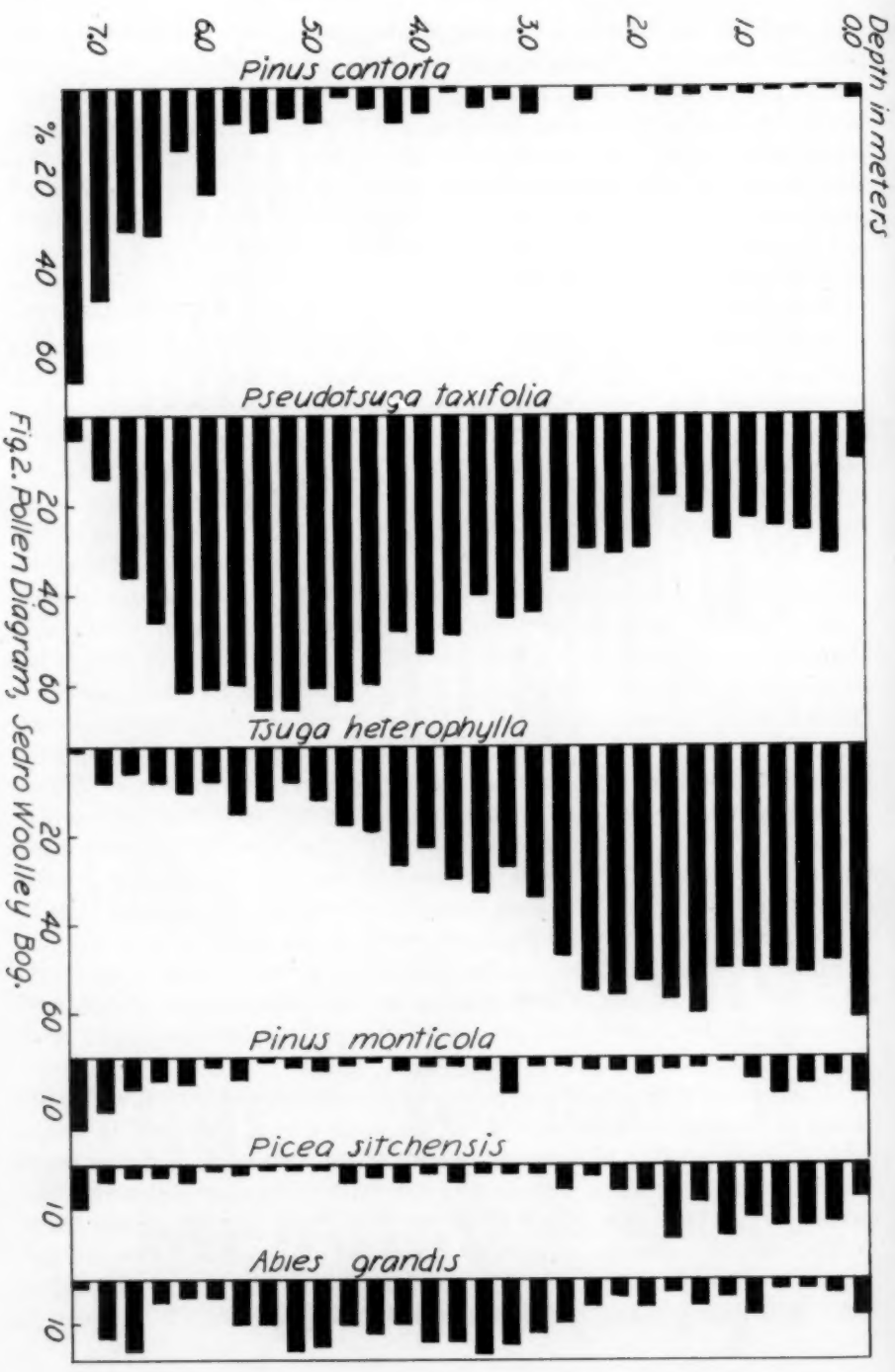

Fig. 2. Pollen Diagram, Sedro Woolley Bog.

the Cascade divide. In the latter region more species are involved and it is much more abundant, since there pine played a far more important role in postglacial forest succession (Hansen 1939a, 1939b, 1939c, 1940b). In the Puget lowland lodgepole and western white pine apparently were pioneer postglacial invaders, and were soon replaced with Douglas fir and western hemlock early in post-Vashon time (Hansen 1938, 1940a).

POSTGLACIAL FOREST SUCCESSION

The pioneer postglacial forests to invade areas adjacent to both bogs consisted largely of lodgepole and western white pine. In the bottom level of the Black Diamond bog the former is recorded as 74 per cent, and in the Sedro Woolley bog as 66 per cent (figs. 1, 2). Western white pine is 18 and 16 per cent respectively in the lowest strata. This record of preponderance of lodgepole pine in early postglacial time corroborates similar evidence indicated by pollen analyses of other bogs in the Puget lowland (Hansen 1938, 1940a). In fact lodgepole pine seems to have been the chief pioneer postglacial invader in most forested regions of the Pacific northwest, regardless of the present climax forest (Hansen 1939a, 1939b, 1940b). In other bogs that may not record all of postglacial forest succession, or are located in glaciated valleys with unglaciated ridges nearby, lodgepole pine is not predominant in the lower levels (Hansen 1939c, 1940c). This suggests that forest succession had already progressed beyond the initial lodgepole pine stage, or that other types of forests persisted on the ridges possibly throughout or at least during the latter part of the glacial period (Hansen 1939c, 1940b). In the Black Diamond bog lodgepole pine maintains a percentage of 70 or more in the lower five levels. It decreases sharply from 70 per cent at 5 meters to 26 per cent at 4.5 meters and continues to decrease with minor fluctuation toward the surface. In the other bog lodgepole pine shows an immediate decrease from the bottom upward to only 8 per cent at 5.75 meters, from which level it is recorded in negligible proportions. The edaphic conditions were probably less favorable for this species in the vicinity of the more northern bog, because of the extensive floodplain area afforded by the numerous streams near their mouths. The well drained, gravelly terrain adjacent to the Black Diamond bog was more favorable for its persistence for a longer period of time. This is further suggested by the greater abundance of lowland white fir and Sitka spruce recorded in the lower strata of the Sedro Woolley bog (figs. 1, 2). Western white pine also diminishes upward in the profiles of both bogs, although it is more abundant near the bottom of the southern bog. This fact is also probably to be correlated with more ideal edaphic conditions in that vicinity.

Douglas fir and western hemlock are sparsely represented in the lower levels of both bogs, but the former abruptly increases inversely with the

decrease of lodgepole pine (figs. 1, 2). In the Black Diamond bog Douglas fir is recorded as only 1 per cent in the lower three horizons and then sharply increases to 50 per cent at 4.75 meters. A more gradual increase is recorded in the other bog, from 5 per cent at the bottom to 62 per cent at 6.25 meters. In the former Douglas fir remains constant with minor fluctuation to 2 meters, where it attains 60 per cent. It reaches its maximum of 63 per cent at 3.75 meters, and then gradually declines from 2 meters to 33 per cent at the top. The Sedro Woolley profile shows that it likewise remained generally constant to 4.5 meters where 60 per cent is recorded, and then diminishes to 18 per cent at 1.75 meters. Again it remains more or less static to 0.25 meter, then decreases to only 10 per cent at the surface. This last decline may be the result of fire or lumbering since the advent of white man.

Hemlock has a lower gradient of increase in the pollen profiles and does not reach its maximum until later than Douglas fir, continuing to increase long after the latter had attained its peak (figs. 1, 2). Hemlock supersedes Douglas fir at 1.25 meters in the Black Diamond bog, and in the other at 2.75 meters. The maximum is reached at the surface in both bogs where 54 and 61 per cent respectively are recorded. In the Sedro Woolley bog hemlock remains predominant to the surface after it supersedes Douglas fir, while in the other both species remain more or less equal except at the surface, where hemlock exceeds Douglas fir by 21 per cent. The increase at the surface may be relative. It would be difficult to estimate the effects of a fire on the Black Diamond bog a decade or so ago. This successional relationship between Douglas fir and western hemlock suggested by the present study further substantiates similar results obtained from other peat profiles in the Puget lowland. It also strengthens the evidence that Douglas fir is a subclimax species, which has persisted as one of the chief dominants in the hemlock-cedar climax since it replaced the initial postglacial forest of lodgepole and western white pine.

Sitka spruce pollen is present in all levels of both bogs. It shows little fluctuation throughout the Black Diamond profile, ranging from 1 to 6 per cent with the higher proportions in the lower half. In the other it plays a more important part, being recorded as high as 17 per cent at 1.75 meters. The higher proportions occur in the upper half of the profile. Fir, which consists chiefly of lowland white fir, is more abundant in the Sedro Woolley bog, being best represented in the lower half of the profile and attaining its maximum of 17 per cent at 3.5 meters. In the other its maximum is 11 per cent at 0.5 meter, and it is consistently low throughout the spectrum. As was previously stated, the extensive lowland area in the vicinity of Sedro Woolley is perhaps responsible for the greater abundance of spruce and fir pollen in that peat deposit. Sitka spruce is one of the chief dominants in the hemlock-spruce climax forest in the fog belt along the Pacific Ocean. Broad-

leaf trees are best represented by alder, and willow and maple are recorded sporadically. Because of their local occurrence these species are probably not indicators of forest succession. Sedge, cattail, waterlily, and ericads are represented in varying quantities and mark the progression of hydrarch succession in the bog itself.

CLIMATIC CONSIDERATIONS

In several earlier papers on pollen analysis of Pacific northwest bogs, the author tentatively suggested a rather complex interpretation of postglacial climate. With the study of additional pollen profiles in this region, a more intensive study of literature dealing with the characteristics, requirements, and distribution of northwest conifers, and observation of them in the field, the conclusion has been reached that the climate has not been the most important factor concerned with postglacial forest succession. Forest succession east of the Cascades may have been influenced more by climate than that in the Puget lowland. Tolerance of shade, longevity, amount and frequency of seed production and age at initial seed production, retention of viability, ability of seed to survive fire, rate of growth, size, adaptability, susceptibility to disease, ability to withstand wind and fire, soil requirements, depth of root system, are some of the characteristics that in their interplay and compromise with one another in the same and different species have largely influenced forest succession. Tolerance of shade, longevity, age at initial seed production, and recovery after extensive fire are perhaps the most important. The present geographic and climatic ranges of the species concerned do not seem to be adequate criteria upon which to base interpretation of climatic trends from pollen profiles. The presence of a species in several regions may reflect different climates, depending upon the ecological relations of its associates. Also, a species may respond differently in areas of similar climate when associated with different species, or edaphic and topographic conditions. It would seem logical to assume that the optimum climate for a species prevails in a region where it makes its greatest sustained growth. Competition, however, may prevent its maximum development in an area of optimum climate, while lack of competition may permit its greater development in a region with less favorable climate. It is realized that all groups of environmental factors, namely physiographic, edaphic, climatic, and biotic, form an intangible, interrelated complex, each factor modifying the effect of the others. Not only may the limiting factor belong to any group, but other factors may assume the limiting role if the balance is altered.

In the hemlock-cedar climax of the Puget Sound basin, intolerance of Douglas fir seedlings for shade is perhaps the principal cause of the subclimax status of this species. Aggressiveness in invading recent burns and cutovers has enabled it to persist as one of the chief dominants during most

of postglacial time. Judd (1915) stated that Douglas fir exists in the Puget Sound region only as a temporary type, which would have vanished long ago if it had not been for the effects of holocaustic fires. A parallel situation exists in northern Idaho, where western white pine likewise has been able to maintain itself in a region normally forested with a climax consisting of western hemlock, western red cedar, and lowland white fir (Hubermann 1935). A pollen profile from this region indicates that this has been true for a large portion of postglacial time (Hansen 1939a).

The pioneer invasion by lodgepole pine may have been partly due to climate and largely due to unstable edaphic and physiographic conditions. The characteristics of lodgepole pine are such that it thrives in a wider range of ecological conditions than other Pacific northwest conifers, which indicates that it can survive in a vacillating environment. Two traits, however, that have prevented it from retaining its initial predominance in the Puget lowland are its intolerance of shade and its relatively short life. In a static environment it is unable to compete with the more tolerant and longer-lived Douglas fir which thrives almost as readily in a sterile soil. The pioneer invasion of deglaciated terrain is attributed to its glacial existence near the ice-front, its early and prolific seed production, retention of seed viability, and ability to germinate in sterile mineral soil left in the wake of the retreating ice. Lodgepole pine produces seed as early as six years, and so can migrate and re-establish itself readily under changing edaphic and physiographic conditions. A tree needing 25 years or more to produce seed would be at a disadvantage before an oscillating ice-front, because it might not reach this period before a radical change in ice-position, drainage, deposition, erosion, or inundation of site destroyed it. Douglas fir and western hemlock would be unable to compete with lodgepole pine because of their greater age before producing seed. As the ice retreated farther and its wasting no longer created unstable edaphic and physiographic conditions, these and less aggressive species gained a foothold. With the moderated and more static conditions, lodgepole was no longer able to compete with the longer-lived and more tolerant Douglas fir, and was replaced. The latter would have been replaced in turn by the more tolerant hemlock and red cedar if forest succession were not periodically interrupted by fire, which caused a reversion to the subclimax type. If we assume that 500 years are necessary for a Douglas fir forest to be converted to the climax type, forest succession must have been interrupted many times during the postglacial time elapsed since the invasion of the first Douglas fir.

While it may be assumed that forest succession progresses under a static climate, nevertheless there probably have been climatic trends during the estimated 25,000 years since deglaciation. The proximity of the ice would in itself afford a cooler climate, because melting ice absorbs considerable heat.

Winds blowing off the ice may have failed to lose their moisture. On the other hand the cooling effects upon the ocean-borne air currents may have caused the latter to lose moisture. The pioneer forests suggest an initial cool and damp climate. The writer believes that it was dryer than the present humid climate. The existence of lodgepole pine in the wet climate along the Pacific Coast may be due to lack of competition by other species that cannot withstand the constant winds and sand-shear, rather than to a hydrophilic nature. The increase of Douglas fir followed by that of hemlock suggests an increase in humidity and temperature to a maximum which may persist to the present. A decrease in humidity in the latter part of the postglacial period is suggested by a sharp decline in Sitka spruce from a high maximum recorded in a pollen profile in southwestern British Columbia, about 60 miles northwest of Sedro Woolley.

The whole problem seems to resolve itself into the question of (1) what degree of species fluctuation in a pollen profile indicates a change in forest composition, and (2) to what extent does a change in the forest composition justify an interpreted climatic trend.

SUMMARY

Postglacial forest succession in the Puget Sound basin evidenced by pollen studies of two post-Vashon bogs about 100 miles apart corroborates the evidence of previous analyses of other peat deposits in the same region.

The pioneer forests consisted chiefly of lodgepole and western white pine. These were replaced rather abruptly by Douglas fir, which was followed by a more gradual increase of western hemlock. In areas adjacent to the Sedro Woolley bog hemlock eventually superseded the former and retained its predominance to the present. In the vicinity of the other peat deposit, Douglas fir and hemlock have remained generally equal as indicated in the upper levels.

Notwithstanding the evidence that forest succession in the Puget Sound basin is largely controlled by non-climatic factors, the author believes there have been several climatic trends, even though slight. The initial climate was perhaps cooler and dryer than the present humid, microthermal type. This was succeeded by an increase in humidity with some warming. The maximum of the latter trend may persist to the present, as there is no indication in the pollen profiles of further change.

Department of Botany
Oregon State College
Corvallis, Oregon

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THE GENUS ORCUTTIA

ROBERT F. HOOVER

The knowledge of *Orcuttia*, a peculiar genus of grasses native to California, until quite recently has been derived from an exceedingly small number of diverse collections from widely separated localities. During the past few years, I have had the opportunity of studying in their native habitat all forms of *Orcuttia* except one. In view of the extremely scanty records previously available to botanists, it seems desirable to place on record the results of these studies.

In 1886 *Orcuttia californica* was discovered by C. R. Orcutt on the coast of Baja California. The plant was recognized by Vasey[1] as representing a genus not previously described and was named for the collector. A collection made in the Sacramento Valley by E. L. Greene in 1890 proved to belong to the same genus but differed so markedly from the Orcutt specimens in certain respects that it was regarded as a distinct species and named, also by Vasey, *Orcuttia Greenei*. For a number of years thereafter, there is no further record of the finding of either of these species. A third collection, made in Shasta County, California, by Miss Alice Eastwood in 1912, was referred at first to *O. californica* but was later recognized as distinct and named *Orcuttia tenuis* by A. S. Hitchcock in 1934. It is rather remarkable that the first three collections of the genus should represent three different species.

It was not until detailed studies of the neglected flora of the Great Valley of California were undertaken that the distribution and ecology of *Orcuttia* became fairly well known. The occurrence of *O. californica* in the Great Valley appears to have been first noted by Klyver[2] in connection with an ecologic study of a transect of the Sierra Nevada in Fresno County. In 1935 I found a plant in Stanislaus and Merced Counties which was described as *O. inaequalis*.[3] Further study has indicated that *O. inaequalis* is merely a geographically segregated variant of *O. californica*. In 1936 more extended field observations established the general distribution of that species in the San Joaquin Valley and also led to the rediscovery in the same region of *O. Greenei*, which had remained unknown since the time of its first collection. In addition, *O. tenuis* was again found in Shasta County, and a fourth species, previously unknown, was collected in Stanislaus County.

The grasses are generally thought to be exceptionally good subjects for herbarium study, because there is less distortion of the tissues in drying than in most groups of plants. However, even if the structural features could be perfectly preserved, proper evaluation of these features would not be

[1] West Am. Sci. 3: 4–6. 1886.
[2] Ecology 12: 1–17. 1931.
[3] Hoover, R. F., Notes on California grasses. Madroño 3: 227–230. 1936.

obtained by examination of dried specimens alone. Questions such as the following would still need to be answered: Which differences among individual plants are directly due to nutrition, and which are independent of environment? In what respects does the plant change as it approaches maturity? When two or more closely related forms occur at the same locality, do they appear genetically distinct, or are they mixed in the same colonies in such a manner as to suggest common parentage? A collector may select plants which illustrate extremes of variation and unintentionally overlook intermediate states. In such cases, field study is needed to demonstrate the existence and the relative frequency of intermediates.

Study of the plants as they grow has tended to minimize the importance of certain differences which have been regarded as specific characters, but at the same time has shown that definite recognizable units actually exist in *Orcuttia*. Sufficient material has been available so that in no instance has it been necessary to define a species on the basis of one collection only or of collections made during a single year. The possibility of confusing seasonal variations with constant entities is thus avoided. The amount of pubescence, which was one of the characters used by Hitchcock[4] as a means of distinguishing species in this genus, is found to be variable among plants which are otherwise identical and therefore is of little significance. Readily recognizable species in this genus are distinguished principally by the arrangement of the spikelets and the nature of the lemma teeth. Other features are often of some importance, but it is necessary to exercise caution in distinguishing between specific differences and individual variation.

The ecological relationships of *Orcuttia* are extremely interesting and offer some puzzling problems for the attention of plant physiologists. All the species occupy the same sort of habitat, growing in clay soil of depressions, popularly called "hog-wallows," which are filled with water during the rainy season but become dry in early summer. The genus occurs most extensively on the east side of the Great Valley of California (Sacramento and San Joaquin Valleys) but extends southward at widely separated localities into northern Baja California. In the Great Valley two of the species are rather common along a narrow strip near the border of the Sierra Nevada foothills. Although numerous "hog-wallow" depressions similar to those inhabited by *Orcuttia* are frequent throughout the width of the valley, no species of *Orcuttia* has been found more than a few miles from the eastern margin. Two possibilities for this peculiar sort of distribution can be suggested. It has been observed that *Orcuttia* occurs nearly always in areas of red soil, chiefly of the San Joaquin series. Assuming that the red color indicates the presence of a large amount of iron, it seems plausible that these grasses may be more sensitive to a deficiency of that element than are most

[4] Manual of the grasses of the United States. 1935.

plants. Another explanation is suggested by the fact that the soil of extensive areas in the Great Valley, except near the eastern margin, contains large amounts of soluble minerals or "alkali." The absence of all species of *Orcuttia* from such areas indicates that these plants may be unable to tolerate either some particular substance or a concentrated soil solution of any sort.

All species of *Orcuttia* reach anthesis in May, when the soil where they grow is still moist but rapidly drying, and bear mature fruit in June and July, after the soil has become dry and hard. The flowers begin to develop at a time when the associated species of *Downingia*, *Allocarya*, and *Mimulus* have for the most part already come to maturity and when *Pogogyne*, *Boisduvalia*, and *Navarretia* are in full flower. The perennial *Eryngium Vaseyi*, which reaches complete maturity even later in the summer, is often the only plant associated with *Orcuttia* and actively growing at the same period, but such annuals as *Cyperus acuminatus* and *Bergia texana* are sometimes components of the same plant society.

Orcuttia tenuis and at least some forms of *O. californica* tend to produce long slender ribbon-like juvenile leaves before the development of the stems. The actual development of such floating leaves, however, depends to a large degree on environmental conditions and is therefore not seen in all specimens. After the soil of the "hog-wallow" depressions has become quite dry, *Orcuttia* develops a hygroscopic viscid secretion having a characteristic odor. This secretion is evidently found in all forms of the genus but is rather sparingly produced in some. The amount of the secretion appears to vary also with the weather, being less noticeable on cool cloudy days. This viscid fluid probably serves to prevent excessive water loss during the development of the fruit and because of its hygroscopic nature may even serve to supply the plant with water from the atmosphere.

The species of *Orcuttia* are, generally speaking, very easily exterminated by the operations of agriculture. With the apparent exception of *O. pilosa*, plowing of the ground where they occur usually prevents the reappearance of these plants in following years. It has been customary in plowing grain fields to pass over depressions which are filled with water for several months, since grain would not grow in such spots. This practice has caused the preservation of *O. Greenei* and *O. californica* at many localities in the San Joaquin Valley. Summer irrigation, however, effectively exterminates these species. With the extensive replacement of wheat and barley by other crops requiring more intensive cultivation, the final disappearance of *Orcuttia* from its native habitat must soon take place.

The phylogeny of *Orcuttia* is obscure. There is an obvious relationship to *Neostapfia*, a very rare monotypic Californian genus which grows in similar situations, often in association with *Orcuttia*. *Neostapfia* is viscid like *Orcuttia* and has the same distinctive odor. There is no clear indication that

any other genus of grasses is closely related to these two genera. It is generally agreed that they are members of the tribe *Festuceae*. Because of its unbranched inflorescence and vernal-pool habitat, I am inclined to believe that *Pleuropogon* is involved in the ancestry of *Orcuttia* and *Neostapfia*, but it is at present impossible to follow the course of evolutionary development in this group of genera. In the spicate inflorescence there is a superficial resemblance to *Sesleria*, an exclusively Old-World genus of perennials, which does not appear likely to be directly related to *Orcuttia*. The striking similarity between *Orcuttia* and *Neostapfia* and the characters of *O. Greenei* indicate the fallacy of classifying *Orcuttia* with such xerophytic genera as *Pappophorum*, in which the lemmas are parted into several awns, although some authors have regarded the awn-like lemma-teeth of *O. californica* as evidence of relationship to such genera. *Orcuttia* is peculiar in that not only the fruit itself but also the florets and the spikelets are persistent after maturity. The fruit is therefore not liberated until the entire plant disintegrates during the following rainy season. This remarkable feature may be regarded as an indication of highly advanced phylogenetic position.

It has been possible to examine material representing all known collections of *Orcuttia* with the exception of the type of *O. Greenei*, of which I have seen a photograph. A few collections were made by the writer to show some biological feature, such as the long juvenile leaves, and are not represented by a full series of specimens. All other known collections of the genus are cited in this article. The material cited is preserved in the following herbaria: California Academy of Sciences (CA), Dudley Herbarium, Stanford University (S), University of California (UC).

ORCUTTIA Vasey, West Am. Sci. **3**: 4. 1886. Annuals with fibrous roots. Plants from pilose throughout to nearly glabrous, at maturity viscid and with a characteristic odor suggesting that of lemons. Stems tufted, fragile at the nodes. Leaves differentiated into sheath and blade but with ligule represented only by a row of hairs, the blades involute in age. Inflorescence spicate. Spikelets compressed, several-flowered, persistent in fruit and the rachilla not disarticulating. Glumes cleft into 2–5 acute teeth or sometimes acute and entire. Lemma with about 11–15 veins, with 5–9 acute or awn-like teeth at apex. Palea with 2 green keels terminating below the obtuse or somewhat three-lobed apex. Each cell of anther with a minute papilla at the base and a short incurved point at apex. Caryopsis small, yellowish, the embryo extending almost the entire length along one side.

TYPE SPECIES: *Orcuttia californica* Vasey.

KEY TO THE SPECIES AND VARIETIES

Spikelets spirally arranged, evenly distributed around the axis; lemma with 5 to 9 very short teeth at apex ..... 1. *O. Greenei*.

Spikelets attached alternately on opposite sides of the axis, thus in two rows; lemma with 5 rather long teeth.

Spike 2 to 5 cm. long, the axis usually not strictly erect; spikelets ascending, tending

to grow toward one side, thus obscuring the two-ranked arrangement; teeth of lemma unequal, the middle tooth longest.

Spikelets borne only on upper third or fourth of stem; glumes 2 to 5 mm. long; lemma 3 to 6 mm. long.

Plant rather sparingly pilose, light green; spikelets 4 to 10, not crowded; (fruit unknown) ..... 2. *O. californica.*

Plant conspicuously pilose, grayish; spikelets 7 to 15, the upper densely crowded; caryopsis 1.3 to 1.75 mm. long.

2a. *O. californica* var. *inaequalis.*

Spikelets often extending as low as middle of stem; glumes 6 to 10 mm. long; lemma 6 to 8 mm. long; caryopsis 2.5 mm. long ..... 2b. *O. californica* var. *viscida.*

Spike 5 to 10 cm. long, the axis strictly erect; spikelets usually appressed to the axis, obviously two-ranked; lateral teeth of lemma equalling the median tooth.

Stems rather stout; leaf-blades when unrolled 2 to 6 mm. wide at widest point; upper spikelets densely crowded, all except the lowermost many-flowered.

3. *O. pilosa.*

Stems slender; leaf-blades when unrolled 1 to 2 mm. wide at widest point; spikelets not crowded, all except the uppermost few-flowered ..... 4. *O. tenuis.*

1. ORCUTTIA GREENEI Vasey, Bot. Gaz. **16**: 146. 1891. Plant not producing long juvenile basal leaves, only slightly glandular at maturity; stems 5 to 30 cm. long, erect or decumbent at base; nodes hairy, often purplish, excessively fragile in fresh plants; leaves more or less hairy throughout or only on the upper surface of the blades, the sheaths shorter than the internodes at maturity; spike 2 to 9 cm. long, enlarged toward apex; spikelets spirally arranged (not two-ranked), the lowest hardly longer than the internodes, the upper congested, with 5 to 15 flowers; glumes 3 to 5 mm. long, toothed or subentire at apex; lemma 5 to 7 mm. long, rather sparingly hairy, broadest below the middle, obliquely truncate and with 2 to 4 very short teeth on either side of the prominent apical point; palea obtusely three-lobed at apex, the veins terminating in the sinuses; anthers 3 to 3.5 mm. long; caryopsis 2.25 to 2.5 mm. long, very minutely but rather conspicuously roughened.

Great Valley of California, near the eastern margin from Tehama County to Tulare County.

CALIFORNIA—TEHAMA CO.: near Vina, *Hoover 2249* (UC). BUTTE CO.: near Chico, 1890, *Greene* (photograph of TYPE, UC). SAN JOAQUIN CO.: Farmington, *Hoover 1302* (CA); 2 miles east of Escalon, *Hoover 1288* (S). STANISLAUS CO.: Paulsell, *Hoover 2441* (UC); 3 miles northwest of Waterford, *Hoover 1582* (CA), *2476* (S); 12 miles east of Waterford, *Hoover 1240* (CA, UC), *3625* (S). MERCED CO.: 2 miles northeast of Planada, *Hoover 2303* (S, UC); 5 miles southeast of Le Grand, *Hoover 1255* (CA). MADERA CO.: 8 miles north of Madera, *Hoover 1251* (CA, UC). FRESNO CO.: 5 miles east of Clovis, *Hoover 2317* (S, UC); 4 miles north of Sanger, *Hoover 1261* (CA). TULARE CO.: Woodlake, *Hoover 1287* (CA).

This species appears to be the commonest of the genus and is remarkably uniform in its characters. Together with species such as *Limnanthes rosea, Downingia ornatissima,* and *D. mirabilis,* it belongs to a well defined group of endemic plants of the vernal pools in the Great Valley of California. The number of lemma-teeth has no taxonomic significance, as it varies within a single spikelet.

From the above citations, it will be noticed that *O. Greenei* apparently occurs in two separate areas, the upper Sacramento Valley and the eastern margin of the San Joaquin Valley. Study of the geographical distribution of other plants occurring in the same region indicates that the range of this species should be continuous. In all probability it has been overlooked by collectors in the lower Sacramento Valley, or perhaps it has already been exterminated in that region.

2. ORCUTTIA CALIFORNICA Vasey, West Am. Sci. **3**: 4. 1886. Plant from sparingly to moderately pilose, evidently without long basal leaves in the typical form; stems 10–50, spreading or ascending, 5–15 cm. long; sheaths of leaves mostly longer than the internodes and concealing the nodes (mature plants not seen); spikes 2–5 cm. long; spikelets alternate on opposite sides of the axis, ascending, tending to be all directed to one side, rather few (4–10), the lower not overlapping and even the upper not densely crowded, with about 4 to 12 flowers; glumes 2 to 4 mm. long; lemma sparsely hairy or nearly glabrous, 4 to 5 mm. long, parted above the middle into 5 subulate teeth, the middle tooth slightly exceeding the lateral; anthers 2 to 2.75 mm. long; fruit unknown.

Coastal region from Riverside County, California, to northern Baja California.

CALIFORNIA—RIVERSIDE CO.: Menifee Valley, *Munz & Johnston 5375* (CA, S, UC). BAJA CALIFORNIA: near San Quentin Bay, *Orcutt 1439* (type collection, S, UC).

The species on which the genus was originally based is the only one which is still very poorly known in the typical form. I suspect that it occurs at other localities in the south but has been overlooked, just as the following variety in the San Joaquin Valley was overlooked for many years.

2a. ORCUTTIA CALIFORNICA Vasey var. **inaequalis** Hoover, comb. nov. *O. inaequalis* Hoover, Madroño **3**: 229. 1936. Plant grayish, rather densely pilose, producing long basal floating leaves which usually disappear at maturity; sheaths of leaves either longer or shorter than internodes; stems from 1 to about 40, erect to spreading, 5–30 cm. long; spikelets 7–15, all except the lowermost densely crowded, with from 4 to as many as 30 flowers; glumes 2–5 mm. long; lemmas hairy, 3–6 mm. long, the teeth conspicuously unequal, awn-tipped, the middle tooth longest; caryopsis about 1.3–1.75 mm. long.

San Joaquin Valley of California, near the eastern margin from Stanislaus County to Tulare County.

CALIFORNIA—STANISLAUS CO.: 3 miles northwest of Waterford, *Hoover 1230* (CA); Montpellier, *Hoover 582* (TYPE, UC), *690* (CA, S, UC), *2599* (CA). MERCED CO.: Ryer, *Hoover 1256* (CA); 2 miles northeast of Planada, *Hoover 2306* (S, UC). MADERA CO.: 8 miles north of Madera, *Hoover 1252* (CA, UC). FRESNO CO.: near Lane's Bridge, *Klyver 1006* (S); 3 miles west of Orange Cove, *Hoover 1273* (CA). TULARE CO.: North Woodlake, *Hoover 1280* (CA).

The observed differences between this plant and typical *O. californica*

are not sharply defined, but it is always possible to distinguish the two. This fact, together with the wide geographical separation, makes it advisable to recognize a variety rather than treating the two forms as a unit.

The variety *inaequalis* is characterized by some striking variations in habit. Although one habit form usually prevails in any given locality, each colony shows sufficient variation to prevent any formal classification on that basis. The most common form in Stanislaus County has short ascending stems. In Madera County a decumbent or prostrate phase is more frequent, while in Tulare County most of the plants are tall and erect. Rarely the spikes are branched.

2b. ORCUTTIA CALIFORNICA Vasey var. **viscida** Hoover, var. nov. Plant tending to produce long juvenile leaves, becoming very viscid; spikes 2–5 cm. long, the spikelets 5–15, more strictly ascending than in var. *inaequalis* and borne farther down on the stem; glumes 6–10 mm. long; lemma 6–8 mm. long, with unequal awned teeth; caryopsis 2–2.5 mm. long.

Planta viscidissima; lemmatibus 6–8 mm. longis, dentibus aristatis; caryopside 2–2.5 mm. longa.

Near the Sierra Nevada foothills in Sacramento County, California.

CALIFORNIA—SACRAMENTO CO.: 2 miles southeast of Orangevale, *Carter 1193* (UC); 7 miles south of Folsom, *Hoover 3709* (UC, TYPE, S).

The long lemmas with awned teeth give to var. *viscida* a distinctive aspect. In view of the geographical proximity of this variety to var. *inaequalis*, the differences between the two show a remarkable contrast to the similarities between var. *inaequalis* and typical *O. californica*. These differences do not seem sufficiently well defined, however, to warrant specific segregation, especially while the size of the caryopsis in typical *O. californica* is not yet known.

3. **Orcuttia pilosa** Hoover, sp. nov. Plant often producing long basal leaves which early disappear, very viscid at maturity, pilose throughout but the backs of the leaves nearly glabrous; stems 4–50, erect but decumbent at base, 5–20 cm. tall, usually in dense tufts; spikes 5–10 cm. long, restricted to the upper half or third of the taller stems but extending nearly to the base of the shortest; spikelets 8–18, two-ranked, strictly erect or slightly curved outward, the upper densely crowded, about 10–40-flowered; glumes about 3 mm. long, irregularly 3–5-toothed; lemmas 4–5 mm. long, parted above the middle into 5 equal teeth, the teeth slightly awn-tipped or merely acute; anthers 2.5–3 mm. long; caryopsis 1.75–2 mm. long.

Planta omnino pilosa, in maturitate viscidissima; culmis 4–50, erectis sed basi decumbentibus, 5–20 cm. altis; spicis 5–10 cm. longis; spiculis 8–18, biseriatis, ca. 10–40 floribus, superioribus dense congestis; glumis ca. 3 mm. longis; lemmatibus 4–5 mm. longis, dentibus aequalibus; antheris 2.5–3 mm. longis; caryopside 1.75–2 mm. longa.

East side of the San Joaquin Valley of California from Stanislaus County to Madera County.

CALIFORNIA—STANISLAUS CO.: 12 miles east of Waterford, *Hoover 1298* (CA), *3624* (UC, TYPE, S). MADERA CO.: 3 miles from Madera on Northfork road, 1938, *Wagnon* (UC); Crocker-Hoffman Ranch, 1938, *Wagnon* (UC).

In general aspect this very rare species is quite different from *O. tenuis*, which it closely resembles in structural details. As long as *O. pilosa* had been found only at one locality in Stanislaus County, there was reason to suspect that it was merely a robust form of *O. tenuis*, and a few specimens were distributed by the writer under that name, but the occurrence of exactly the same form in Madera County indicates that it is a well defined and constant entity and therefore worthy of taxonomic recognition. This conclusion is supported by geographical considerations. Within their widely separated ranges, *O. tenuis* and *O. pilosa* vary only within definite limits and never simulate each other in appearance, although it is difficult to find an entirely convincing morphologic basis for their segregation.

4. ORCUTTIA TENUIS A. S. Hitchcock, Am. Jour. Bot. **21**: 131. 1934. Plant under favorable conditions producing long floating juvenile leaves, becoming very viscid at maturity, 5–15 cm. tall; stems 1–18, slender, strictly erect or when crowded decumbent at base; leaves thinly pilose throughout or sometimes only on the upper surface of the blades; spike 5–9 cm. long, extending usually below the middle of the stem, often nearly to the base; spikelets 6–12, not crowded, strictly erect, sparsely pilose or sometimes glabrous, with 2–10 flowers (all except the uppermost few-flowered), the lower distant; glumes 3–5 mm. long, with 2–5 teeth at apex; lemma 4.5–6 mm. long, parted above the middle into 5 equal awn-tipped teeth; anthers 2.75–3.5 mm. long; fruit unknown.

Shasta and Tehama Counties, California, east of the Sacramento River.

CALIFORNIA—SHASTA CO.: Goose Valley, *Eastwood 1013* (type collection, CA, UC); 5 miles east of Redding, *Hoover 2268* (S, UC); 4 miles north of Anderson, *Hoover 1210* (CA, UC). TEHAMA CO.: volcanic plateau northeast of Red Bluff, *Hoover 4097* (CA, S, UC).

Orcuttia tenuis comes into flower somewhat earlier than the species occurring farther south in the Great Valley, thus reversing the order of development observed in most genera. Under the original description, the habitat of *O. tenuis* was said to be "open sandy soil," but that appears to be an error. The species always grows in beds of vernal pools, so far as I have observed. The slender erect stems, bearing spikelets nearly to the base, are distinctive.

NORTH AMERICAN RANUNCULI—I

LYMAN BENSON

The following series of articles[1] is a presentation of data on the North American *Ranunculi* occurring north of the Mexican boundary of the United States. It consists of detailed geographical ranges, determination of type specimens, new names and new combinations, descriptions of varieties not included in Abrams Illustrated Flora of the Pacific States **2**: 1940 with the opposed characters of the typical species, and citation of a few significant specimens for misunderstood or rare species. In order to show the bases for reorganization of species and varieties and to facilitate reference of plants to the proper categories, keys are included.

The first paper deals with the first seven species and a complex of varieties of the subgenus *Eurananunculus*, section *Chrysanthe*, as delimited by Benson; cf. Am. Jour. Bot. **23**: 26–33, 169–176. 1936. **27**: 799–807. 1940.

SECT. 1. CHRYSANTHE (SPACH) L. BENSON

KEY TO THE SPECIES

Achene beaks not over 2 mm. long, regularly-curved or hooked.

Fruiting receptacle not more than 2.5 times the length in anthesis; head of achenes hemispherical or globose.

Petals large and conspicuous, 6–18 mm. long, at least twice as long as the sepals.

Stems rooting at the nodes ..... 3. *R. repens.*

Stems never rooting adventitiously (except at some subterranean nodes near the stem base in *R. californicus* var. *cuneatus.*

Stem base a conspicuous, bulb-like, subterranean thickening 6–7 mm. long by 10–13 mm. in diameter ..... 4. *R. bulbosus.*

Stem base not bulbous.

Sepals spreading; petals clawless or nearly so; stems unbranched in the first 2–3 dm.

Achene beak 0.3–0.6 mm. long ..... 1. *R. acris.*

Achene beak 1.2–1.7 mm. long ..... 2. *R. acriformis.*

Sepals reflexed at or below the middles (except in *R. occidentalis* var. *Turneri*); petals with claws; stems usually branched in the first 2 dm.

Achenes 1–3 or rarely 3.5 mm. long.

Petals 5–6 or rarely 7–9 or 12, the blades 1–2 or rarely 2.5 times as long as broad ..... 5. *R. occidentalis.*

Petals 9–16 or 26, rarely fewer, the blades 2–2.5 times as long as broad. 6. *R. californicus.*

Achenes 3.5 or usually 4–5 mm. long; petal blades 1–2 or, in a variety, 2–2.5 times as long as broad ..... 7. *R. canus.*

[1] This is the first of a series of five articles dealing with the taxonomy of North American *Ranunculi.*

Petals minute, 4 mm. long or less, or 4–6 mm. in a rare southern Colorado variety of *R. Bongardii;* petals and sepals of about equal length.

Receptacle conspicuously hairy, usually 3–4 mm. long in fruit.

Nectary scale forming a pocket one-fourth the size of the petal; stem base bulbous, the plant perennial; herbage hirsute; achenes finely reticulate; cauline leaves simple, parted and toothed, the teeth obtuse ..... 8. *R. recurvatus.*

Nectary scale not forming a pocket, free laterally; stem base unknown, the plant perhaps annual; herbage glabrous; achenes somewhat rough-reticulate (on a much larger pattern); cauline leaves pinnately 3-foliolate, the lateral parts simple or 2–3-toothed ..... 10. *R. Macounii.*[2]

Receptacle glabrous; nectary scale not forming a pocket, free laterally, much less than one-fourth the size of the petal; stem base not bulbous; cauline leaves parted and lobed, the lobes acute ..... 9. *R. Bongardi.*

Fruiting receptacle at least 3 times the length in anthesis, hispid; head of achenes ovoid or cylindrical.

Sepals equal to or a little shorter than the petals, the petals 3 or 5–7 mm. long; head of achenes ovoid, 7–9 mm. long; stems often rooting at the nodes. 10. *R. Macounii.*

Sepals about twice the length of the petals, the petals 2–3 mm. long; head of achenes cylindrical, 11–17 mm. long; stems never rooting adventitiously. 11. *R. pennsylvanicus.*

Achene beaks 2–4 mm. long, straight or bent but not regularly curved and not hooked at the tips for more than 0.1 mm. (cf. also *R. occidentalis* vars. *dissectus* and *Howellii*); receptacle hispid.

Petals 8–18; roots of the main fascicle all alike (*R. fascicularis* var. *cuneiformis* has 7–9 petals, but it has the roots of the main fascicle differentiated into two types). 12. *R. macranthus.*

Petals 5 or 6.

Roots of the main fascicle all alike, not differentiated into two types.

Sepals reflexed.

Petals 4–7 mm. broad, rarely narrower; stems usually 1.5 mm. or more in diameter (except in *R. Bloomeri,* which has usually emarginate petals).

Petals not emarginate; leaves at least sparsely hairy.

Sepals two-thirds or three fourths the length of the petals; leaflets of the radical leaves 3 or the leaves simple; plants often stoloniferous in summer. 16. *R. septentrionalis.*

Sepals half the length of the petals; leaflets of the radical leaves 3–7; plants never stoloniferous ..... 13. *R. orthorhynchus.*

Petals usually emarginate; leaves glabrous, shining ..... 14. *R. Bloomeri.*

Petals 2–3 or rarely 4 mm. broad; stems 0.7–1.5 or 2 mm. in diameter; plant subglabrous ..... 15. *R. carolinianus.*

Sepals spreading (rarely reflexed in *R. septentrionalis,* as shown in the key above).

Sepals two-thirds or three-fourths the length of the petals; plant often stoloniferous in summer; achene keel well-marked; plant usually, but not always, either subglabrous or sparsely hairy ..... 16. *R. septentrionalis.*

Sepals half the length of the petals; plant never stoloniferous; achene keel obscure; plant always markedly hairy ..... 17. *R. hispidus.*

Roots of the main fascicle of two kinds, some filiform (about 0.5 mm. in diameter) and some fleshy or tuberous and 1–5 mm. in diameter ..... 18. *R. fascicularis.*

[2] A reduced form occurring along Peace River.

1. RANUNCULUS ACRIS L. Sp. Pl. 554. 1753. Pastures, meadows, and roadsides at low elevations or up to 1,000 or 1,300 meters elevation in the Western mountains; Europe; naturalized in North America at Kodiak and King Cove, Alaska and from British Columbia to Saskatchewan and to Western Washington, Oregon (Salem, Brooks, and Union), and Missouri; Minnesota and northern Illinois to Labrador and New England and south on the Atlantic coastal plain to North Carolina; Greenland and Iceland.

Type collection: "Habitat in Europae *pratis, pascuis."*

A European form called *Ranunculus acris* var. *Stevenii* (Andrz.) Lange has been distinguished by its less-dissected leaves with broadly oblanceolate or more-or-less cuneate segments. This form occurs in the Craigmyle District, Alberta, and from Quebec to Newfoundland, Nova Scotia, New England, and New York, and is occasional elsewhere. According to the viewpoint of the writer, the characters of this plant do not entitle it to recognition as a variety.

According to a note by Ora Parker Phelps, Rhodora **21**: 208. 1919, *Ranunculus Boraeanus* Jordan, Obs. Pl. Crit. (6) 19. 1847, a Central-European relative or variety of *R. acris* with finely-dissected leaves, was found in 1919 at Gansevoort, New York. It was identified by Dr. M. L. Fernald.

2. RANUNCULUS ACRIFORMIS A. Gray, Proc. Am. Acad. **21**: 374. 1886. Wet meadow land at 2,000–2,500 meters elevation; reported from Alberta; Sweetwater County to Laramie County, Wyoming; Laramie River in Colorado. Plains grassland. June and July.

Type collection: "R. acris, Hook. Fl. i. 18, & Lond. Jour. Bot. vi. 66, not L.—Northern Rocky Mountains, lat. 58°, *Drummond.* Wyoming, *Parry* (distrib. as R. affinis). Wind River, *Dr. Forwood,* and near Cheyenne, *Greene."* Hooker, l.c., cites the Drummond specimen as follows: "Banks of rivers in the central limestone district, and eastern primitive range, from Canada to lat. 58°, *Drummond."*

Significant specimens: COLORADO: Laramie River, *Crandall* in 1891, NY, US. IOWA: Belmond, *Whited* in 1903, WSC (questionable identification).[3]

3. RANUNCULUS REPENS L. Sp. Pl. 554. 1753. *R. Clintonii* Beck, Bot. N. & Mid. St. 9. 1833.

[3] The symbols used for the herbaria in which specimens are located are as follows: S, Dudley Herbarium, Stanford University; NY, New York Botanical Garden; GH, Gray Herbarium, Harvard University; US, United States National Herbarium; UW, University of Washington; T, J. W. Thompson, Seattle, Washington; WSC, Washington State College; UO, University of Oregon; WILL, Willamette University; OSC, Oregon State College; UC, University of California; J, W. L. Jepson, University of California; CA, California Academy of Sciences; SBM, Santa Barbara Museum; P, Pomona College; ISB, University of Idaho Southern Branch; UA, University of Arizona; SAC, U. S. Field Station, Sacaton, Arizona; COLO, University of Colorado Museum; F, Mr. O. A. Farwell, Lake Linden, Michigan; B, Lyman Benson, University of Arizona; MINN, University of Minnesota; MICH, University of Michigan; CORN, Cornell University; K, Kansas State College of Agriculture and Applied Science; HGr, Herbarium Greeneanum.

Stems prostrate,[4] rooting adventitiously at practically every node, 1–50 dm. long and 0.7–1.5 mm. in diameter, not fistulous, appressed-hairy in the typical form; leaf blades compound, deltoid-cordate in outline, 1.5–6 cm. long, 2–8 cm. broad, pinnate with 3 sessile or petiolulate leaflets, which are proximally cuneate and distally lobed and toothed but acute in outline, middle petiolule up to 4 cm. long, the lateral petiolules up to 2 cm. long; petals 5, 7–13 mm. long; achenes 20–25 in a subglobose head; receptacle subglobose-ovoid.

Meadows and marsh borders at low altitudes or up to 1,500 meters in the Rocky Mountains; Europe; naturalized in North America from the south coast of Alaska to coastal California as far south as Carmel River (also at Cobb Valley in Lake County, at Quincy, Bear Valley, and Pine Ridge (Fresno County) in the Sierra Nevada, and at Goose Lake); Rocky Mountain System in Custer County, Idaho and at Denver, Colorado; Quebec to Newfoundland and North Carolina. May to September.

Often a lawn weed, the prostrate habit and adventitious roots cheating the mower.

Type collections: (1) *R. repens*, "*Habitat in* Europae *cultis.*" (2) *R. Clintonii*, "Hab. Banks of Canal near Rome, Oneida Co., N. Y."

Dr. M. L. Fernald, Rhodora **21**: 169. 1919, gives the following key for segregation of the varieties of *R. repens:*[5]

A. Middle leaflet of the basal leaves cuneate to subtruncate at the base: petals 5–9; stamens numerous ..... B.

B. Lobes and teeth of the leaves deltoid or obovate to oblong, obtuse or bluntish.

Trailing or repent branches or stolons present.

Stems and petioles distinctly pubescent.

Pubescence appressed ..... *R. repens* L.

Pubescence wide-spreading ..... Var. *villosus* Lamotte.

Stems and petioles glabrous or nearly so ..... Var. *glabratus* DC.

Trailing or repent branches wanting ..... Var. *erectus* DC.

B. Lobes and teeth of the much-cleft leaves lanceolate to linear, acuminate. Var. *linearilobus* DC.

A. Middle leaflet of the basal leaves rounded or subcordate at the base: petals very numerous, forming a "double" flower ..... Var. *plentiflorus* Fern.

R. repens var. *villosus* LaMotte is the common spreading-hirsute form of the species. On the Pacific Slope it is the dominant form, and, in fact, the typical species is uncommon or even rare (collected only as follows: Salem,

[4] Wherever abbreviated descriptions are given under the name of the species alone they apply to the typical variety and not to the species as a whole.

[5] While the validity of the philosophy behind the use of the formal name "var. *typica*" is admitted, it is the opinion of the author that publication of formal trinomials for typical varieties is unnecessary. The long-established custom is to consider the plant described under the specific name as the typical variety within the species and to give varietal names to only the other varieties of the species.

Oregon, *J. C. Nelson 225;* Noyo, Mendocino County, California, *Duncan 181;* Alhambra, California, *Mrs. J. D. Abrams*). However, according to the viewpoint of the writer, the "var. *villosus*" is not worthy of recognition as a variety.

3A. RANUNCULUS REPENS L. var. GLABRATUS DC. Prodr. **1**: 38. 1824. Similar to but even more robust than var. *erectus* and perhaps not distinct from it; stoloniferous; stems up to 7 or 9 dm. long; leaf blades up to 10 or 11 cm. long and 13 cm. broad, petiolules as much as 2.5 cm. long; flowers in an extreme form subcymose; petals 5; receptacle and head of achenes sometimes ovoid-cylindrical.

European plant naturalized in wet places here and there from Quebec and Newfoundland to New England and New Jersey; Farmington and Salt Lake City, Utah, May to August.

The extreme form is so strikingly different from *R. repens* as to seem to be another species, but intermediates are more common than the extremes.

Type collection: None given, European.

Significant specimens (representative of the extreme form): NEWFOUNDLAND: Force le Plain, Harry's Brook, *R. B. Kennedy 336*, GH. QUEBEC: Carleton, *Collins, Fernald, & Pease* in 1904, GH. UTAH: Farmington, *M. E. Jones* in 1881, NY, *Clemens* in 1908, GH. NEW JERSEY: Closter (?), *unnamed collector* in 1861, GH. MASSACHUSETTS: Wellesley, *Gilbert* in 1894, GH; Nantucket, *Day 4* in 1900, GH; Botanic Garden of Harvard University in 1862, GH.

3B. RANUNCULUS REPENS L. var. ERECTUS DC. Prodr. **1**: 38. 1824. Growing often in shallow water of meadow or marsh land: naturalized in the Puget Sound Region and southward at scattered stations mostly near the ocean coast to Curry County, Oregon; Santa Cruz, California; occasional in Quebec and Newfoundland. May to July. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collection: None given, European.

R. repens var. *linearilobus* DC. occurs sparingly in New England. The following specimens are in the Gray Herbarium: Cutler, Maine, *Kennedy, Williams, Collins, & Fernald* in 1902; Waverly Oaks, *Gray Herbarium Local Collection*, 1894; Nantucket, Mass., *Day 13* in 1900. According to the viewpoint of the writer, this form is not worthy of recognition as a variety. The status of the plant is about the equivalent of that of *R. acris*, var. *Stevenii*, since there is only the degree of dissection of the leaves to distinguish it.

3C. RANUNCULUS REPENS L. var. PLENIFLORUS Fern. Rhodora **19**: 138. 1917. Wet ground, an occasional escape from gardens in New York, New England, and Maryland; Liberty, Kittitas County, Washington. May to July. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collection: "Frequent in old gardens, and tending to become naturalized in meadows and along roadsides, Oneida, Herkimer County, New York, May 30, 1900, J. V. Haberer, no. 1530 in Gray Herb.

"This plant is generally called in horticulture *R. repens*, var. *florepleno* but the latter name (if it can be accepted as a valid name) belongs to the double-flowered European form of *R. repens* with the bases of the leaflets cuneate to subtruncate, as in true *R. repens*, and the teeth and segments elongate and subacute to acuminate. The history of var. *pleniflorus* is obscure. It is found in old gardens and as a somewhat naturalized weed in eastern America; but such illustrations of the double-flowered *R. repens* of Europe as the writer has seen, as far back as Gerard's Herball (ed. Johnson, 1633), where the plant is figured as *Ranunculus dulcis, multiplex*, and Besler's Hortus Eystettensis (1613) where it is called *Ranunculus hortensis, multiflorus*, show the characteristically cuneate-based leaflets of *R. repens*."

4. RANUNCULUS BULBOSUS L. Sp. Pl. 554. 1753.[6] Dry fields and roadsides at low elevations; Europe; naturalized in North America at Revelstoke, British Columbia, St. John's, Newfoundland, Shelbourne, Nova Scotia, Bingen, Washington, Salem, Oregon, Fortuna, California, Oquauka (?) Illinois, Keneewaw County, Michigan, Lake Maxinkuckee, Indiana, Knoxville, Tennessee, Red River, Louisiana, and Stumptown, West Virginia and from New York and New England to Bryan County, Georgia. May and June.

Type collections: (1) *R. bulbosus*, "*Habitat in* Europae *pratis, pascuis.*" (2) Var. *petiolulatus*, "No. 5568. In und um Norfolk häufig." "Im Mai & Juni 1890, botanisierte ich um Norfolk." Virginia, *Krause*.

THE RANUNCULUS OCCIDENTALIS COMPLEX

The *Ranunculus occidentalis* group is perhaps only scarcely less difficult to classify than the races of dogs. There are no wholly reliable characters for segregation of the species *R. occidentalis*, *R. californicus*, and *R. canus*, and wherever geographic ranges meet all three species and their 10 varieties seem to cross-pollinate freely, or at least the plants in the field show abundant evidence of character recombinations. However, the large fruit of *R. canus* is fairly reliable for distinguishing it from the other two species, and the number of petals serves to segregate all but a small percentage of the plants of *R. californicus* and its three few-petaled varieties from *R. occidentalis* and its sometimes 5–8- or rarely 9–12-petaled varieties *Rattanii* and *Eisenii*. Table 1 summarizes the tendencies in these three species.

5. RANUNCULUS OCCIDENTALIS Nutt. in Torr. & Gray, Fl. N. Amer. **1**: 22. 1838. *R. occidentalis* var. *robustus* A. Gray, Proc. Am. Acad. **21**: 373. 1886. *R. tenuipes* Heller, Muhlenbergia **1**: 50. 1904. *R. occidentalis* var. *laevicaulis* Suksdorf, West Am. Sci. **15**: 58. 1906.

Stems erect or suberect, 2–7 dm. long, 1.5–3 mm. in diameter, freely branching; radical leaf blades simple, rather thick, 1.5–3.5 cm. long, 2–4.5 cm. broad, 3-parted or rarely -divided, the lobes cuneate, again lobed, the ultimate lobes usually not triangular, the sides commonly curving, proximally cordate and distally rounded or acute; petals 5 or rarely 6–8, narrowly

[6] Two old-world varieties are distinguished from the typical one by Fernald, Rhodora **42**: 451–452. 1940.

TABLE 1

	R. occidentalis	*R. californicus*	*R. canus*
Petal Number (Fairly reliable)	5–6 or in 3 vars. sometimes 5–8 or 12.	9–16 or 26 or in 3 vars. 5 or 7–12.	5–10 or in 1 var. 10–23.
Petal Shape (Less reliable)	1.5–2 or rarely 1.1 or 2.5 times as long as broad.	2–2.5 times as long as broad.	1–2 times as long as broad; 1 var. 2–2.5.
Fruit Size (Fairly reliable)	2.5 × 2 mm. or in vars. up to 3 × 2.5 or even 3.5 × 3.3.	2–2.8 × 1.8–2.3 mm. or in 1 var. 1–2 × 1–1.5.	4–5 × 3–4.5 mm. or rarely smaller.
Achene beak (Less reliable)	1.2–1.8 mm. long or in 2 vars. 0.5–1.3; 2 vars. 1.5–2.	Usually 0.4–0.8 mm. or in 1 var. 1–1.5.	0.3–0.6 or 1 mm.
Plant Size (General tendency)	Smaller, except vars. *Eisenii, montanensis,* and *Nelsonii.*	Larger, except var. *cuneatus.*	Largest, also herbage more commonly silky-villous.
Compound leaves (General tendency)	Rare, except var. *Eisenii.*	Common, except vars. *gratus* and *cuneatus.*	Common in var. *laetus,* otherwise uncommon.

elliptic, 1.5–2 times as long as broad (claw 1–3 mm. long), 8–12 or rarely 18 mm. long, 3.5–5 or 8 mm. broad, the nectary scale glabrous, free for nearly the whole length, 0.7 mm. long, truncate; each achene obovate-discoid, 2.5 mm. long, 2 mm. dorsoventrally, 0.3–0.4 mm. laterally, glabrous, the achene beak slender, 1.2–1.8 mm. long, falcate, usually barely recurved, prolonging the ventral margin of the achene body.

Mostly beneath trees or on vernally moist prairies or hillsides; Pacific Slope from Alaska to the Umpqua River Valley, Oregon; inland along the Columbia River to west Klickitat County, Washington and The Dalles, Oregon; Port Orford, Oregon. Northwestern coniferous forest. Late April and May.

This species, *R. canus, R. californicus,* and their varieties have an abundance of connecting forms. A form with petals 15–18 mm. long by 7–8 mm. broad occurs at The Dalles and near Eugene, Oregon.

Type collections: (1) *R. occidentalis,* "Plains of the Oregon (Columbia) River, near woods, *Nuttall!* Dr. Scouler!; Sitcha, *Bongard!*" The Nuttall specimen at Columbia University (New York Botanical Garden) has been designated as a LECTOTYPE (cf. Heller, Muhlenbergia **1**: 51. 1904.) (2) Var. *robustus, R. occidentalis* A. Gray, Proc. Amer. Acad. **8**: 374. 1872, not. Nutt in 1838. "A collection of plants made in Oregon by ELIHU HALL during the summer of 1871." (3) *R. tenuipes, Heller* "No. 3935, collected June 13, 1898 at Montesano, Chehalis [Gray's Harbor] county, Washington, altitude about 200 feet." (4) Var. *laevicaulis,* "An verschiedenen Stellen mit her gewöhnlichten Form vermengt, bei Bingen, Washington, 30 März 1886 und später (Nr. 1972)," *Suksdorf.*

Significant specimens of *Ranunculus occidentalis* and its varieties: see L. Benson, Am. Jour. Bot. **23**: 28–29. 1936.

5A. RANUNCULUS OCCIDENTALIS Nutt. var. RATTANII A. Gray. Proc. Am. Acad. **21**: 373. 1886. *R. Rattanii* Howell, Fl. N. W. Am. **1**: 17. 1897.

Openly wooded hills and prairies; inner part of the seaward coast ranges from Coos and western Josephine Counties, Oregon to Mendocino and western Lake Counties, California. Borderland between the Northwestern coniferous forest and the oak woodland. April to June. Cf. L. Benson in Abrams, Ill. Fl. Pac. Sts. **2**: 1940.

The hispid achene is to be found in any of the southern varieties of *R. occidentalis*, as well as in *R. californicus* and *R. canus*. It is not necessarily a feature of var. *Rattanii* or of any other variety. This variety is rather striking in the extreme form but throughout the seaward side of the distributional range it intergrades with *R. californicus* var. *gratus*, and in the north it passes into *R. occidentalis* var. *Howellii* and in the south into the variety *Eisenii*.

Type collection: "N. California on the Klamath, Rattan." The TYPE specimen in the Gray Herbarium is labelled as follows: "Common on the Klamath, Calif. *V. Rattan*, June, 1879."

5B. RANUNCULUS OCCIDENTALIS Nutt. var. EISENII (Kell.) A. Gray. Proc. Am. Acad. **21**: 373. 1886. *R. Eisenii* Kell. Proc. Calif. Acad. **7**: 115. 1876.

Vernally moist ground in the California foothills and mountain valleys at 100–1,300 meters or up to 2,200 meters elevation in Kern County, beneath oaks (leaves simple) or in vernal meadows and rivulets (leaves compound); Weaverville; eastern Mendocino, Lake, and eastern Napa Counties; Sierra Nevada foothills and Greenhorn and Tehachapi Mountains; West Butte, Sacramento Valley. Oak woodland. Late February to May or June. Cf. L. Benson in Abrams Ill. Fl. Pacif. St. **2**: 1940.

The form of *R. occidentalis* growing from southeastern Jackson County and southwestern Klamath County, Oregon, to Shasta County, California, is intermediate between the varieties *Eisenii* and *ultramontanus*. The variety *Eisenii* intergrades freely with *R. californicus* at Healdsburg and at the south base of Mt. St. Helena, where 5-petalled and 9–16-petalled plants are found growing together. The compound-leaved forms from vernal meadows and the simple-leaved forms from oak woodland maintained their characters when transplanted by the writer to identical environments in adobe soil at Menlo Park, California. A glabrous, dissected-leaved form (L. Benson 6316) was found growing in water at Stubbs Ranch Junction north of Lower Lake, Lake County.

Type collection: cf. Proc. Calif. Acad. **7**: 89. 1876, "Dr. Eisen, of Sweden, placed in our hands for determination his plants from near Fresno, Cal." The type is unknown, and it may have been destroyed in the San Francisco earthquake and fire of 1906. However, according to Curran, Bull. Calif. Acad. **1**: 130. 1885, it disappeared much earlier. The following is her statement, "*Ranunculus Eisenii* Kellogg, Proc. Cal. Acad. vii. 115. Probably *R.* NELSONII var. TENELLUS, Gray, but the specimen has disappeared from the herbarium, and the identification is not certain." The following information has been received from Dr. Eric Hultén, Botaniska Museet, Lund, Sweden, "As far as I have been able to find there is no specimen of *Ranunculus Eisenii*

in Swedish herbaria. I have never seen any Californian specimens collected by Eisen in Swedish Museums." We adopt the interpretation of Dr. Gray, Proc. Am. Acad, **21**: 373. 1886. His reference is to a plant identified by Torrey as *R. canus* Benth.; cf. Torr. Pac. R. R. Rep. **4**: 62. 1857. The collection was cited as follows: "Hill sides, Duffield's Ranch, Sierra Nevada; May 11." The specimen in the Gray Herbarium was collected by Bigelow.

5C. RANUNCULUS OCCIDENTALIS Nutt. var. ULTRAMONTANUS Greene, Pittonia **3**: 13. 1896. *R. alceus* Greene, Erythea **3**: 69. 1895. *R. ultramontanus* Heller, Muhlenbergia **6**: 11. 1910. *R. occidentalis* var. *alceus* Jepson, Fl. Calif. **1**: 540. 1922.

Meadows and along mountain streams at 1,300–2,000 meters elevation in the North Coast Ranges of California from Elk Mountain, Lake County, northward, and at 1,800–2,300 meters largely on the eastern side of the Sierra Nevada from Mt. Shasta to Inyo County and to near Reno and Carson City, Nevada; continuing northward in modified form and occurring at a few stations east of the Cascade Mountains in Southern and Central Oregon. Yellow pine forest. June and July. Cf. L. Benson in Abrams Ill. Fl. Pacif. St. **2**: 1940.

Type collections: (1) *R. alceus*, "Collected at an altitude of about 4,000 feet on Elk Mountain, Mendocino [Lake] Co., Calif., July, 1892, by Mr. Jepson." Elk Mountain is in Lake County. This error was corrected by Jepson, Fl. Calif. **1**: 540. 1922, "type loc. Elk Mt., Lake Co., Jepson." The type has not been located in the Herbarium Greeneanum or in Dr. Jepson's working collection. (2) Var. *ultramontanus*, "Banks of streams and lakes, or in moist meadows along the Truckee River, at the eastern base of the Sierra Nevada, Calif." The Herbarium Greeneanum has only one specimen collected by Dr. Greene prior to 1896, and it is chosen as a LECTOTYPE. It was obtained near Boca on the Truckee River, California, on July 24, 1895 (HGr 2726).

5d. RANUNCULUS OCCIDENTALIS Nutt. var. DISSECTUS Henderson, Rhodora **32**: 25. 1930. *R. ciliosus* Howell, Fl. N. W. Amer. **1**: 17. 1897. *R. marmorarius* Jepson & Tracy in Jepson, Fl. Calif. **1**: 542. 1922.

Meadows of mountains and high plains at 1,300–2,200 meters elevation; Eastern Oregon and the Rogue River-Umpqua River Divide; Marble Mountain, Siskiyou County, California. Yellow pine forest. June and July. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collections: (1) *R. ciliosus*, "Moist banks, in Bear Valley, Blue Mountains, Oregon. *Howell*, May 23, 1885." (2) *R. marmorarius*, "Marble Mt., western Siskiyou County [California], Chandler (type)." *Chandler 1891.* (3) Var. *dissectus*, "Dry slopes of Crater Lake Park, OREGON, near Pole Creek Bridge, where collected by *Lyle Wynd*, July 12, 1928. His no. 2221."

5E. RANUNCULUS OCCIDENTALIS Nutt. var. HOWELLII Greene, Pittonia **3**: 14. 1896. *R. Howellii* Greene in Howell, Fl. N. W. Am. **1**: 17. 1897.

Openly wooded hills at 300–1,300 meters; Rogue River watershed in Jackson and Josephine Counties, southwestern Oregon. Northwestern coniferous forest and oak woodland. Late March to May or June. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collection: "Dry hillsides near Ashland, Oregon, 1899; collected by Mr. Howell." *Howell 1331.*

5F. RANUNCULUS OCCIDENTALIS Nutt. var. **montanensis** (Rydb.) L. Benson, comb. nov. *R. montanensis* Rydb. Mem. N. Y. Bot. Gard. **1**: 166. 1900.

Stems erect or decumbent at the bases, 3–6 dm. long and 3–7 mm. in diameter; radical leaves simple, semicircular in outline, 2–5 cm. long, 3–10 cm. broad, 3-divided or nearly so, the divisions again 3–5-lobed and proximally narrowly cuneate and distally acute, pilose with spreading or somewhat appressed hairs, the ultimate lobes acute, but not triangular, the sides curving; petals 5, rarely 10, 8–11 mm. long, 6–7 mm. broad, 1.2–1.5 times as long as broad; achenes 15–45 (the other varieties 8–20), achene body obovate, 2.5 mm. long, 2 mm. broad, glabrous, the beak about 1 mm. long, recurved, falcate, often bent rather sharply at the middle; receptacle globose, 2.5 mm. long in fruit (about 1.5 in the other varieties.)

Wet meadows, 1,500–2,500 meters elevation; Boise, Custer, and Blaine Counties and Beaver Canyon, Idaho; western Montana; western edge of Wyoming; Albuquerque, New Mexico (?). Yellow pine forest. June and July.

Closely related to *R. acriformis* A. Gray and to *R. occidentalis* var. *Nelsonii.*

Type collection: "MONTANA: Helena, 1891, *F. D. Kelsey* (type)."

5G. RANUNCULUS OCCIDENTALIS Nutt. var. **Nelsonii** (DC.) L. Benson, comb. nov. *R. recurvatus* Poir. var. *Nelsonii* DC. Syst. **1**: 290. 1818. *R. Nelsonii* A. Gray, Proc. Amer. Acad. **8**: 374. 1872. *R. repens* L. var. *major* Nakai, Bot. Mag. (Tokyo) **42**: 23. 1928. *R. Nelsonii* subsp. *insularis* Hult. Svensk. Bot. Tidskr. **30**: 526. 1936.

Stems erect, 4–7 dm. long, usually 2–6 mm. in diameter, branching above, the lowest internode usually 1.5–3 dm. long, strongly fistulous, hirsute; radical leaf blades simple, 2.5–4.5 cm. long, 2.5–7 cm. broad, deeply 3-parted and each primary part again 3–9-lobed or -toothed, proximally cordate and distally rounded or obtuse in outline; sepals 5 or in 1 specimen some flowers with 6; petals 5–6, 7–9 mm. long, the nectary scale glabrous, free laterally, the non-glandular portion 3–5 times as broad as long, truncate; each achene asymmetrically obovate, 3 mm. long, 2.5 mm. dorsiventrally, 0.5 mm. laterally, glabrous, the achene beak about 0.6 mm. broad at the base, 1.2–2 mm. long, recurved, commonly markedly falcate.

Moist ground at low elevations along the cost of Alaska and in the Aleutian Islands. Northwestern coniferous forest. June and July.

Type collections: (1) Var. *Nelsonii,* "In insulâ Unalaskâ unâ ex Aleutienis. D. Nelson." (2) Var. *major.* According to Hultén this variety is *R. Nelsonii.* According to information supplied by Dr. H. W. Rickett of the New York Botanical Garden, "Nakai's collections are from Corea. Other collections which he cites are from Sachalin, Kuriles, Yeso." (3) Subsp. *insularis.* The following is quoted from Hultén by Dr. Rickett; Aleutian Islands: Amchitka, July 9, 1932. Hn No. 6463 (type). ("Distributed to several European and American Museums.")

5H. RANUNCULUS OCCIDENTALIS Nutt. var. BREVISTYLIS Greene, Pittonia **3**: 14. 1896.

Practically glabrous; primary divisions of the radical leaf blades only 3–4-lobed or -toothed; sepals 5, reflexed; petals 5 usually narrowly obovate, emarginate or rounded, 7–10 mm. long, 5–6 mm. broad, the nectary scales only 1.5–2.5 times as broad as long, apically rounded; base of the achene beak 0.4–0.5 mm. broad; similar otherwise to var. *Nelsonii*.

Moist ground; Yes Bay and Loring, southern tip of Alaska. Northwestern coniferous forest. Summer.

Significant specimens: ALASKA: Yes Bay, *Howell 1602, HGr*, NY, S; Loring, Chamberlain 26 in 1903, NY.

5I. RANUNCULUS OCCIDENTALIS Nutt. var. **Turneri** (Greene) L. Benson, comb. nov. *R. Turneri* Greene, Pittonia **2**: 296. 1892.

Hirsute; primary divisions of the radical leaf blades 3-lobed, "the lateral lobes bifid, all incisely cleft;" sepals 5, spreading; petals 5, broadly obovate, truncate, 12–14 mm. long, the nectary scale unknown; achene beak long and slender, recurved.

Moist ground; Porcupine River, Northeastern Alaska. Northern coniferous forest. Summer.

Type collection: "We are glad to be able to dedicate so fine a new plant to the gentleman who has given the very best of recent contributions to our knowledge of Alaskan vegetation, Mr. J. H. Turner, who brings it from Porcupine River." TYPE, *Turner* in 1891, *HGr 2811*.

5J. RANUNCULUS OCCIDENTALIS Nutt. var. **hexasepalus** L. Benson, var. nov. Hirsute; primary divisions of the radical leaf blades 5–13-lobed or -toothed; sepals usually 6 (a number unique in *Ranunculus*) reflexed; petals 8–12, obovate or narrow, distinctly emarginate, 11–13 mm. long, 3–4 or 7–8 mm. broad, the nectary scale once or twice as broad as long, truncate or obtusely pointed; fruit unknown.

Hirsuta; partibus primariis folii 5–13 lobatis; sepalis plerumque 6, reflexis; petalis 8–12, obovatis, emarginatis, 11–13 mm. longis, 3–4 vel 7–8 mm. latis; squamulis nectarii latis.

Moist ground; Queen Charlotte Islands, British Columbia. Northwestern coniferous forest. Summer.

Type collection: Queen Charlotte Islands, *Rev. J. H. Keen 10* in 1898. TYPE in the New York Botanical Garden.

Significant specimens: BRITISH COLUMBIA: Queen Charlotte Islands, *Boas 86* in 1901, NY; Skidegate (?) Inlet, Queen Charlotte Islands, *Newcombe* in 1897 (*Geol, Surv. Can. 18054*), *HGr 2993*.

6. RANUNCULUS CALIFORNICUS Benth. Pl. Hartw. 295. 1848. *R. Deppei* Nutt. in Torr. & Gray, Fl. N. Amer. **1**: 21. 1838, as syn. *R. dissectus* Hook. & Arn. Bot. Beech. Voy. 316. 1840. Not Bieb. in 1819. *R. californicus* var. *latilobus* A. Gray, Proc. Am. Acad. **21**: 375. 1886. *R. latilobus* Parish, Pl. World **20**: 214. 1917.

Vernally moist land of north slopes, meadows, fields, and rolling hills; seaward coastal ranges from Humboldt County, California to Ensenada, Baja California; inland from San Francisco Bay to the Sierra Nevada at Volcano, Amador County and the foothills east of Madera. Oak woodland. Late January to May.

A form with the floral parts resembling vegetative leaves occurs in adobe soil in the San Francisco Bay Region. North Coast Range varieties of *R. occidentalis* and *R. canus* occasionally exhibit the same tendency. A five-petalled form occurs in San Diego County. (Laguna Mts., *Munz 9705, Sanford* in 1927; Julian, *M. E. Jones* in 1906, *J. D. Randall* in 1914; Santa Ysabel, *Henshaw* 200.) This form might be included in *R. occidentalis* var. *Eisenii* because of the presence of only 5 petals. However, the other characteristics seem to agree with those of the form of *R. californicus* growing in the San Jacinto Mountains and in the mountains of San Diego County. This form has unusually small fruit. In vegetative characters it agrees more fully with *R. canus* var. *Ludovicianus* than with *R. californicus*.

Type collections: (1) *R. Deppei*, "*R. acris* (Linn.) . . . β. hairy; petals oblong, 10–14.—R. Deppei *Nutt.! mss.* . . . California, *Nuttall!* June." (2) *R. dissectus*, "California-Supplement. Where not otherwise mentioned, it is to be understood that the following species are from the collection of Mr. Douglas. They were presented by the Horticultural Society of London, in whose service Mr. Douglas was at the time he gathered them." (3) *R. californicus*, *Hartweg* "1628 (155) . . . *R. dissectus*, Hook. et Arn. Bot. Beech. p. 316, non. Bieb.—In sylvis prope Monterey," collected in 1846–7. An isotype from Hartweg's collection (Gray Herbarium) is the same peculiar dissected-leaved form as the plant upon which *R. dissectus* was based (isotype also in the Gray Herbarium). No other collections of the species quite match these two isotypes! (4) Var. *latilobus*, "A common coarse-leaved and more robust form, *R. Ludovicianus* Greene, Bull. Calif. Acad. ii. 58." Greene, Fl. Fran. 300. 1892, wrote as follows: "Var. (4) *latilobus*, A. Gray, Proc. Am. Acad. xxi. 375 (1886), in part, excl. *R. Ludovicianus*. . . . Var. 4 is n. 374 of the State Survey from Santa Barbara." Gray's brief description throws no light on the subject, and he gave no indication that *Brewer 374*, Geological Survey of California, from Santa Barbara was the type of his variety. However, it is not likely that he had seen the type of *R. Ludovicianus*, since none of the original material of it is at the Gray Herbarium or apparently elsewhere. Furthermore, in the Synoptical Flora of North America (**1**: 35. 1895) the variety *latilobus* is said by Robinson to be "a common form, especially southward, from San Francisco Bay to San Diego and San Bernardino," while *R. Ludovicianus* (now transferred to *R. canus* as a variety) is confined to fairly high elevations of the Tehachapi and San Bernardino Mountains in the interior. The description in the Synoptical Flora is too general to be of value in determining the identity of the variety. However, the material at the Gray Herbarium labelled for the Synoptical Flora as var. *latilobus* is definitely typical *R. californicus*. Since the Synoptical Flora label is on *Brewer 374*, the writer accepts it as representative of the plants to which the name *latilobus* was given, because Robinson was in a better position than anyone else to know what Gray intended. It is to be noted that Parish (l.c. 1917) took up the name *latilobus* as a specific epithet intended for var. *Ludovicianus*. Otherwise, interpretations have been generally the same as Greene's and Robinson's.

6A. RANUNCULUS CALIFORNICUS Benth. var. GRATUS Jepson, Fl. W. Mid. Calif. 201. 1901.

Wet banks and bottom land of deep canyons or moist north slopes; Curry County, Oregon to Napa County and the Monterey Peninsula in California.

Northwestern coniferous forest (inner edge of the redwood belt). Late February to May. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

This variety appears to pass into *Ranunculus occidentalis* var. *Eisenii* in Mendocino, Sonoma, and Napa Counties and into *Ranunculus californicus* from Sonoma County southward. It is best-developed in Sonoma and Santa Clara Counties, and the extreme form is strikingly differentiated from *Ranunculus californicus*. Segregation of the variety in Mendocino County and northward is difficult.

Type collection: "Commonly in wooded country: hills of Napa Valley; Vaca Mountains."

6B. RANUNCULUS CALIFORNICUS Benth. var. CUNEATUS Greene, Fl. Fran. 299. 1892. *R. californicus* var. *crassifolius* Greene, Erythea **1**: 125. 1893.

Barren sea bluffs; Sauvies Island, Columbia River, Oregon to Monterey County, California; Santa Maria, San Miguel, and Santa Cruz Islands. Northwestern coniferous forest region. May and June. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Oregon specimens tend toward 5 petals and compound leaves. They are as closely related to *R. occidentalis* as to *R. californicus*.

Type collections: (1) Var. *cuneatus*, "Var. 3 is confined to the wet meadows that lie back of the ocean in San Mateo Co., doubtlessly also reaching San Francisco Co. In cultivation at Berkeley it behaves very unlike the other forms, is almost annual, i.e. many individuals come to flowering the first year from seed, and die before the end of the year. Other individuals are of perennial duration." No type was found by the writer at the Herbarium Greeneanum, Notre Dame University. Specimens cultivated at Berkeley by Dr. Greene in 1893 and 1894 are at the Herbarium of the University of California. These were pressed one and two years after publication of the variety. However, they represent perhaps the stock from which the variety *cuneatus* was described, and they are the nearest approach to a type. (2) Var. *crassifolius*, "Collected at Fort Bragg, Mendocino Co., Calif., by Mr. Michener." The type of this variety also failed to be located at the Herbarium Greeneanum, and the writer has seen no isotype.

6C. RANUCULUS CALIFORNICUS Benth. var. RUGULOSUS (Greene) L. Benson, Am. Jour. Bot. **23**: 30. 1936. *R. rugulosus* Greene, Pittonia **2**: 58. 1890.

Wet sand of rivers and ditches up to 1,000 meters elevation; California; tule land along the Sacramento River in Sutter County; San Joaquin Valley from western Merced County to Kings and Tulare Counties; lower Sierra Nevada foothills from Tuolumne County to Mariposa County. March to May. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Type collection: "The type of this species is a very slender but tall plant from the Chowchilla Mountains in the eastern part of south-central California, where it was collected in 1875 by Mr. F. P. McLean." The "Chowchilla Mountains" are a ridge in the Sierra Nevada west of Wawona, Yosemite National Park. The TYPE is HGr 2799.

7. RANUNCULUS CANUS Benth. Pl. Hartw. 294. 1848. *R. occidentalis* Nutt. var. *canus* A. Gray, Proc. Am. Acad. **8**: 374. 1872. *R. californicus* Benth. var. *canus* Brew. & Wats. Bot. Calif. **1**: 8. 1876. *R. canus* var. *Blankinshipii*

Rob. in A. Gray, Syn. Fl. N. Am. **1**: 35. 1895. *R. Blankinshipii* Heller, Muhlenbergia **1**: 40. 1904. *R. longilobus* Heller, Muhlenbergia **2**: 36. 1905.

Heavy soils of hills and valleys at 20–300 meters elevation; California; inner Coast Ranges from Tehema County to the Mt. Diablo Range; Sacramento Valley; lower Sierra Nevada foothills (below the oak belt) from Butte County to Tuolumne County; San Joaquin Valley in San Joaquin County and at Merced and Lindsey. Late February to early April. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

The name *Ranunculus canus* is taken for the plants of the *R. occidentalis* complex having fruit 4–5 mm. long. In the Coast Range and the Sierra Nevada foothills it is not unusual to find on the same plant the large fruit of *R. canus* and the (usually) relatively small, simple leaves of *R. occidentalis* var. *Eisenii*, which grows in both ranges at higher elevations or at stations more remote from the Sacramento Valley than does *R. canus*. This form has been named *R. canus* var. *Blankinshipii*.

Type collections: (1) *R. canus*, "In paseuis humidis vallis Sacramento ubi terram late obtegit." *Hartweg 1626* (*239*) in 1847. Jepson, Erythea **5**: 54. 1897, quotes the following from Hartweg: "On April 13, I left [the junction of the Yuba and Feather Rivers] with Mr. L. for his farm seventy miles higher up the valley. . . . Crossing Feather River, which here is eighty yards broad, and of considerable depth, our course lay five and twenty miles along that river, through a beautiful wood of evergreen and deciduous oaks. . . . Leaving Feather River we struck across a prairie for twenty miles; here immense fields of *Eschscholtzia crocea*, *E. californica* and *Ranunculus No. 239*, presented themselves, each species growing by itself." The junction of the Yuba and Feather Rivers is at the present town of Marysville; Oroville is 26 miles up the Feather River; Chico is 21 miles northwest of Oroville. The country between Oroville and Chico is treeless grassland. The type station for *R. canus*, therefore, must be between Oroville and Chico. A few collectors have obtained the species on the plains and foothills between the towns in recent years. (2) Var. *Blankinshipii*, "Capay, Yolo County, Calif., J. W. Blankinship. 15 April, 1893." (3) *R. longilobus*, "The TYPE is [*Heller*] no. 7912, collected May 31, 1905 on hills about one mile back from Middle Creek Station near Keswick, Shasta county, California, growing in damp ground near a little stream." This plant is intermediate in vegetative characters between *R. occidentalis* vars. *Eisenii* and *ultramontanus*, and both the type collection and a specially-collected topotype (*Heller 13930*) show fruit partly of the *R. canus* type and partly of the *R. occidentalis* var. *Eisenii* type. While *R. longilobus* is placed in synonymy under *R. canus*, the type is by no means identical with that species. The Middle Creek Station plants seem to represent a local population derived by recombination of characters of *R. canus* and *R. occidentalis* vars. *Eisenii* and *ultramontanus*. It is doubtful if the population is sufficiently homogeneous and consistently differentiated to be considered as a separate variety. However, this point might be determined by intensive field work at and near the type locality. Herbarium specimens are inadequate for such a study.

7A. RANUNCULUS CANUS Benth. var. LAETUS (Greene) L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940. *R. californicus* Benth. var. *laetus* Greene, Fl. Fran. 299. 1892. *R. californicus* var. *canescens* Greene, Fl. Fran. 299. 1892. *R. hesperoxys* Greene, Erythea **2**: 189. 1894. *R. canus* var. *hesperoxys* Davis, Minn. Bot. Stud. **2**: 475. 1900.

Heavy adobe soil on north slopes of foothills; California; Marysville Buttes; Woodland; Vaca Mountains; Mt. Diablo Range; San Joaquin Valley near Stockton. March and early April. Cf. L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940.

Intermediates between the variety and *R. canus* occur in the Sacramento Valley. West and south of the Mt. Diablo Range, the leaf form of var. *laetus* is found combined with the characteristics (small fruit and 9–16 narrower petals) of *R. californicus*.

Type collections: (1) Var. *laetus*, "Var. 1 is of the interior, about Suisun . . . occupying low meadow lands adjacent to brackish marshes." Greene's specimen collected at Suisun on May 4, 1890 is designated as a LECTOTYPE (HGr 2542). (2) Var. *canescens*, "Var. 2 belongs to middle elevations of the Mt. Diablo Range and the valleys among them, from Niles to the hills east of Livermore, thence southward to San Luis Obispo County. It was in part my *R. Ludovicianus*." The following specimens are at the Herbarium Greeneanum: near Livermore, *Greene*, March 9, 1889 (HGr 2528–9); Paso Robles, *C. C. Parry* in 1888 (HGr 2527). Since there is no material from Niles, the first-mentioned locality, the Livermore specimen is designated as a lectotype. The Parry specimen is densely hairy like var. *laetus*, but the fruit and flower characters place it in *R. californicus*. (3) *R. hesperoxys*, "This is the plant, which in the *Flora Franciscana* and in the *Manual*, I called *R. canus*, for the reason that it seemed to come nearer the description of that species than any other plant known to occur in the region whence Mr. Bentham had his type. But having now seen that type, I am prepared to assert that *R. canus* had not yet been rediscovered. Nothing at all resembling Hartweg's plant is known to Californian botanists of the present time." In *Flora Franciscana* (301. 1892) *R. canus* is said to occur on "Plains and hills of the interior, especially about Antioch, and northward to Chico, *Mrs. Bidwell*." The following specimen is designated as a LECTOTYPE: Antioch, *Greene*, April 6, 1887 (HGr 2615).

Representative specimens: CALIFORNIA: Marysville Buttes, *L. Benson 6352*, B; Woodland, *Blankinship* in 1893, GH; Gordon Valley, Napa County, *Greene* in 1886, *HGr;* Suisun, *Greene* in 1885, *HGr*, UC., in 1895, *HGr*, UC.; Antioch, *Greene* in 1887, *HGr*, UC, in 1895, *HGr*, UC. Davy 915, *HGr;* Mt. Diablo, *Greene* in 1886, *HGr;* Livermore, *Greene* in 1889, *HGr;* Knight's Ferry, *Bancroft* in 1895, J, *HGr;* San Joaquin County, *Stanford*, S.

7B. RANUNCULUS CANUS Benth. var. LUDOVICIANUS (Greene) L. Benson in Abrams, Ill. Fl. Pacif. St. **2**: 1940. *R. ludovicianus* Greene, Bull. Calif. Acad. **2**: 58. 1886. *R. californicus* var. *ludovicianus* Davis, Minn. Bot. Studies **2**: 476. 1900.

Moist ground of vernal meadows or rivulets or mountain streams at 1,000–2,300 meters elevation; Temblor, Greenhorn, Tehachapi, San Gabriel, and San Bernardino Mountains of South-Central and Southern California. Yellow pine forest and oak woodland. Late March to May. Cf. L. Benson in Abrams Ill. Fl. Pacif. St. **2**: 1940.

Type collections: (1) *R. ludovicianus*, "High valleys among the mountains of San Luis Obispo County, California, and eastward to Tehachapi Pass. Collected by Mrs. Curran, in 1884." Neither the Brandegee Collection at the University of California nor the Herbarium Greeneanum contains a specimen collected by Mrs. Curran (Brandegee) in San Luis Obispo County, and no specimen of this variety has been collected in San Luis Obispo County at any other time. The epithet *ludovicianus* has been consistently applied to the common many-petalled plant growing in the Tehachapi Mountains, and the writer believes that, in absence of a type, established custom should be law. The 1884 collection from Tehachapi by Mrs. Curran (Brandegee) is designated as a LECTOTYPE, and, in the event that it is not rediscovered, the 1895 collection by Mrs. Brandegee (Herbarium of the University of California) should be considered a substitute for it. The 1884 specimen is to be found in neither the University of California Herbarium nor the Herbarium Greeneanum. *Ranunculus californicus* var. *latilobus* is an epithet attributed by some botanists to this plant (cf. discussion under *R. californicus*).

DEPARTMENT OF BOTANY, UNIVERSITY OF ARIZONA,
TUCSON, ARIZONA

VARIABILITY IN WOOD STRUCTURE IN ROOTS OF NATIVE ONTARIO CONIFERS

M. W. Bannan

(WITH EIGHTEEN FIGURES)

INTRODUCTION

The present paper is one of a series on the wood structure of conifers. Its scope is limited to consideration of variability in the secondary xylem of roots of such native species as *Thuja occidentalis*, *Tsuga canadensis*, *Abies balsamea*, *Larix laricina*, *Picea glauca*, *P. mariana*, *Pinus Banksiana*, and *P. Strobus*. Material was collected from trees in different types of habitat and from different parts of the root systems, so that some conception might be obtained of the range of variation within the individual, the differences between trees in varied habitats, and the relationships, if any, between wood structure and environment. The bearing of the variability in structure upon the identification of coniferous woods, both living and fossil, is discussed.

The root systems of the native conifers differ. *Larix laricina* and *Picea mariana* under most conditions, and *Thuja occidentalis* and *Picea glauca* when growing in swamps, have shallow root systems made up largely of widely spreading horizontal roots confined to the top few inches of soil. In dry soils, especially sand, *Thuja*, *Picea glauca*, and *Pinus* spp. generally have sinker roots in addition to the laterals. These deep roots include the tap root, when present, and other roots which extend downward from the principal horizontal roots. In the following descriptions these deep roots are designated as vertical roots, and the horizontal roots located close to the surface as lateral roots.

GROWTH RINGS AND SIZE OF TRACHEIDS

The width of the growth rings was found to be highly variable. Of adjacent rings one sometimes was wide while those preceding or succeeding were narrow. Some rings were more or less uniform in width around the circumference, others were decidedly eccentric. The greatest eccentricity was observed in certain lateral roots near the stem, and in vertical roots wedged between stones. On the other hand, many lateral roots, and most vertical roots growing in sand, were more or less round.

Generally the growth rings were wider in roots growing in wet soils than in dry sand. In material of *Thuja*, *Tsuga*, *Larix*, and *Picea mariana* the average differences in ring width between roots from wet and dry sites ranged from 25 to 50 per cent.

The proportion of early and late wood in the growth rings, the size of the tracheids, and the thickness of their walls, varied greatly in different parts of the root system and in different specimens. The study of large numbers of roots revealed some correlation between character of the wood and location in the root system, and sometimes with the depth in the soil, but it should be emphasized that the wood structure was exceedingly variable, even in different parts of the same root.

Usually, the largest tracheids and the least development of late wood were observed in the inner wood, to a distance of 1 cm. or more from the primary xylem, in the distal parts of lateral roots of mature trees. This type of wood was best developed in these lateral roots located in the upper few inches of soil, but at no point exposed, and several feet distant from the bole (fig. 3).

A more stem-like wood in which the tracheids were smaller in diameter, the walls thicker, and late wood more extensive (figs. 1, 2), was found in the following kinds of roots or in roots growing under the following conditions: (1) the wood in the proximal portions of the roots of small trees two or three feet high; (2) the wood on the upper side of large buttress roots belonging to mature trees; (3) the outer wood, around the whole circumference, of some of the larger lateral roots, both close to and as far as ten feet or more from the stem; (4) the wood formed on the upper side of lateral roots after they have been uncovered by soil erosion, irrespective of size of the root or distance from the stem; (5) some of the more or less superficial lateral roots of adult trees growing in meadows or swamps which tended to become dry during the summer; (6) certain of the vertical roots extending down into the ground.

The above descriptions hold generally for the conifers listed in the introduction, but there was evidence that the range of variation in various parts of the root system and in roots growing under varied environmental conditions was greater in some species than in others. For instance, the average differences in size between the tracheids of lateral and vertical roots were much greater in *Picea* spp. than in *Thuja occidentalis* (table 1).

The nature of the factors involved in the development of the stem-like type of wood in some roots was not clear, although certain circumstances were noted which evidently played some part. For instance exposure of certain roots resulted in a change in wood structure. An example in which

Explanations of figures 1–5.

FIG. 1. *Picea glauca.* Stem-like wood in vertical root, 3 feet deep in uniform sand. × 40. FIG. 2. *Picea mariana.* Stem-like wood in vertical root wedged between stones. × 40 FIG. 3. *Picea glauca.* Open type of wood in lateral root 24 feet from the stem, approximately 2 inches deep in sand. × 40. FIG. 4. *Picea mariana.* Abnormal tissue in lateral root. × 150. FIG. 5. *Picea mariana.* Alternate and opposite arrangements of pits in the radial walls of tracheids in lateral root. × 330.

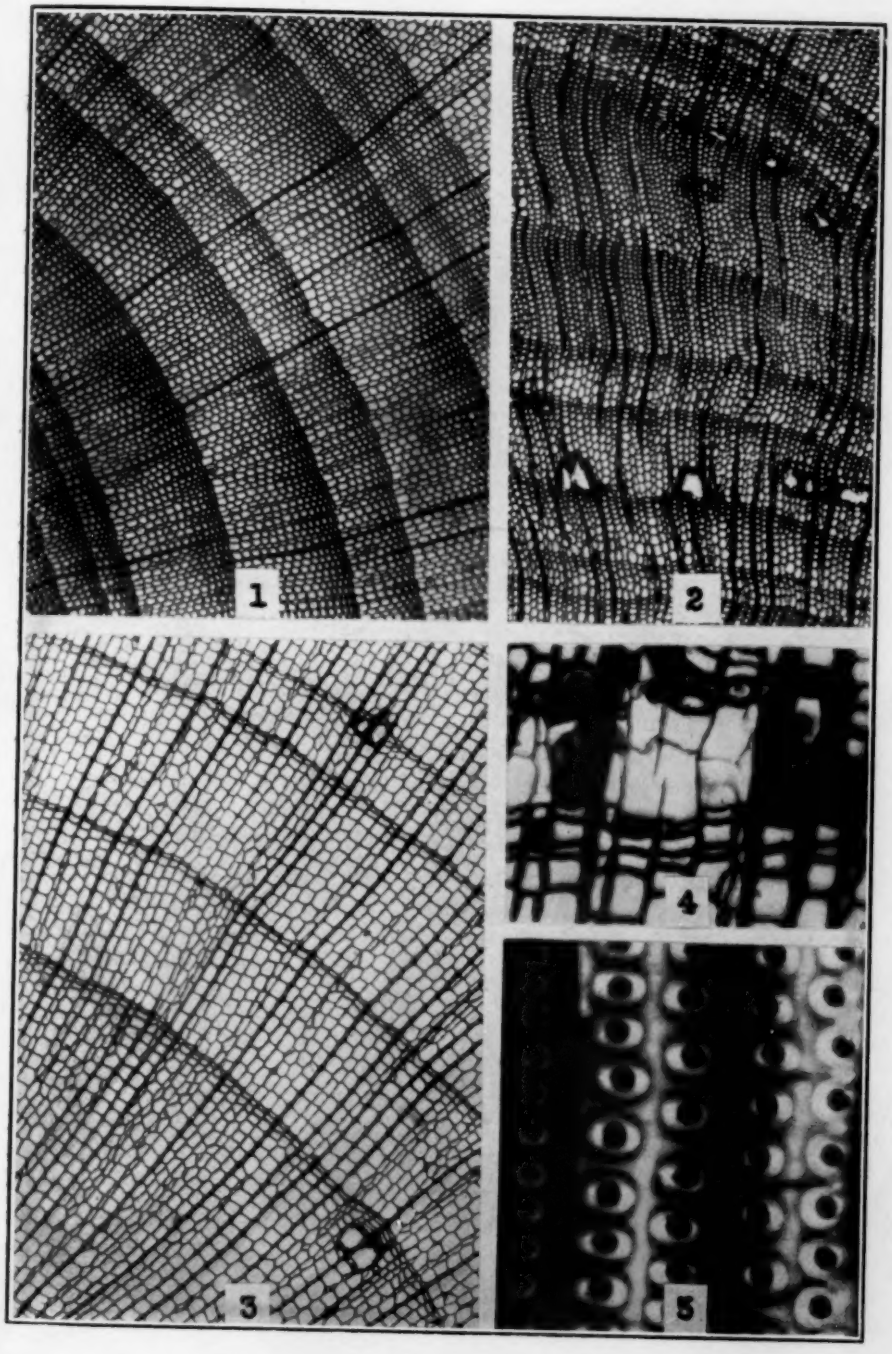
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TABLE 1

Average radial and tangential dimensions of early-wood tracheids in root wood at distances of 1 to 3 mm. from the primary xylem

Species	Lateral roots	Vertical roots
Thuja occidentalis (67 roots)	42 × 27 μ	40 × 25 μ
Picea mariana (53 roots)	48 × 29 μ	36 × 23 μ
Picea glauca (42 roots)	46 × 28 μ	34 × 22 μ

such a relationship was indicated has been described and illustrated in a previous article (Bannan 1937) for *Thuja occidentalis*. Similar correlation was observed in exposed lateral roots of other genera.

On the other hand, some circumstance other than exposure was evidently operating to produce the stem-like wood found in some roots well below the surface of the ground. Certain vertical and oblique lateral roots of *Picea*, located at depths of 1–2 feet in gravelly and stony soils, exhibited a transition from a more or less open type of wood near the center to a fine-textured stem-like wood in the outer rings. Vertical roots of such western species as *Pinus ponderosa*, *Tsuga heterophylla*, and *Libocedrus decurrens* excavated from gravel were also found to resemble in this respect the roots of *Picea* described above. In most roots the change in wood type took place while they were still quite small, not more than 1 or 2 cm. in diameter.

In other vertical roots of *Picea* (*P. glauca*) the wood was stem-like from the center. Such a uniform stem-like wood was observed in roots growing at depths of 2–4 feet in medium or coarse sand without gravel or stones. On the other hand, vertical roots of *Tsuga canadensis* at similar depths in fine sand were less stem-like. In these roots the wood varied considerably from one specimen to another, and even in different parts of one growth ring at the same level in the root. Considerable variation was also found in vertical roots of *Thuja occidentalis* at like depths in fine sand. Some of the roots exhibited a transition from an open wood near the center to a rather stem-like wood in the outer rings, but in others the wood was more or less uniformly intermediate in character. The factors responsible for these differences were not determined.

The age of the tree appeared to have some influence upon the wood structure. The wood in the proximal parts of the roots of small trees up to 2 or 3 feet in height was usually stem-like. The youth of the trees suggests that here some ontogenetic factor was involved.

Another circumstance having some effect on the wood structure, particularly in the lateral roots of mature trees, was distance from the stem. In most of the forms studied late wood was less extensively developed and the tracheids became larger in diameter at increasing distances from the bole. The extent of this tracheid enlargement is illustrated in figure 13 for *Larix*

and *Picea*. In *Thuja*, on the other hand, there was little difference. No measurements were made of the tracheids in roots of *Tsuga canadensis*, *Pinus Banksiana*, or *P. Strobus*, but the trend appeared to be similar to that illustrated for *Larix* and *Picea*.

No consistent relationship was discovered between the size of the tracheids in lateral roots and the amount of soil moisture. Measurements were made of some 70 roots of *Larix laricina*, collected from four sites, two wet and two dry. The radial and tangential dimensions of the early-wood tracheids in the inner wood, at distances from 6 to 19 feet from the stem, were as follows: $64 \times 34\ \mu$ in roots growing in a swamp in southern Ontario; $60 \times 32\ \mu$ in roots on elevated ground nearby, the soil a mixture of silt and sand; $71 \times 37\ \mu$ in roots growing in water-soaked muck at the bottom of a creek flowing through a larch, black-spruce swamp in northern Ontario; $63 \times 36\ \mu$ in roots on a neighboring sand plain where no water was encountered in excavations as much as 4.5 feet deep, the soil a medium or coarse sand.

In both comparisons between wet and dry sites the tracheids were slightly larger in the roots growing in swamps. However, a trend in the opposite direction was observed in the roots of *Picea mariana*. Here the tracheid dimensions in lateral roots obtained from three sites were: $43 \times 27\ \mu$ in swampy silt-sand soil in southern Ontario; $46 \times 29\ \mu$ in dry medium or coarse sandy soil, northern Ontario; $54 \times 29\ \mu$ in dry gravelly soil, northern Ontario.

In *Thuja occidentalis* very little difference was discovered between roots in wet and dry soils. Roots were collected from a number of sites in southern Ontario, and the average measurements were $42 \times 29\ \mu$ in dry soils (sandy hilltops), and $42 \times 26\ \mu$ in cedar swamps. All the values represent the outside dimensions of the tracheids, that is the distances between the middle lamellae. The measurements were based upon the early-wood tracheids in the inner wood, 1–3 mm. from the primary xylem, in lateral roots at points 6–19 feet distant from the stem.

The observations recorded fail to indicate the existence of any consistent relationship between tracheid size and soil moisture. Diverse tendencies appeared in the species studied, and much dissimilarity was found between trees of the same species growing under like soil conditions, and sometimes between roots of the same tree.

A search of the literature revealed that some work has been done on the texture of wood in stems, but apparently none on roots. Harlow (1927), reporting on tracheid diameters in stem wood of *Thuja occidentalis*, found greater variation between trees on the same site than between the averages of two extreme sites, though the trees on limestone soil had slightly smaller tracheids than trees on a peat bog. Myer (1930) found the intra-regional

variation to be much greater than the inter-regional variation. The average tangential diameter of tracheids in the stem of *Tsuga canadensis* growing on a spruce flat was 4.4 per cent greater than in trees on a slope, but on the latter a 17 per cent variation was observed. According to Kienholz (1931) tracheids in the wood of *Pinus contorta* were larger in trees in sphagnum bogs than on other sites.

TRACHEID PITTING

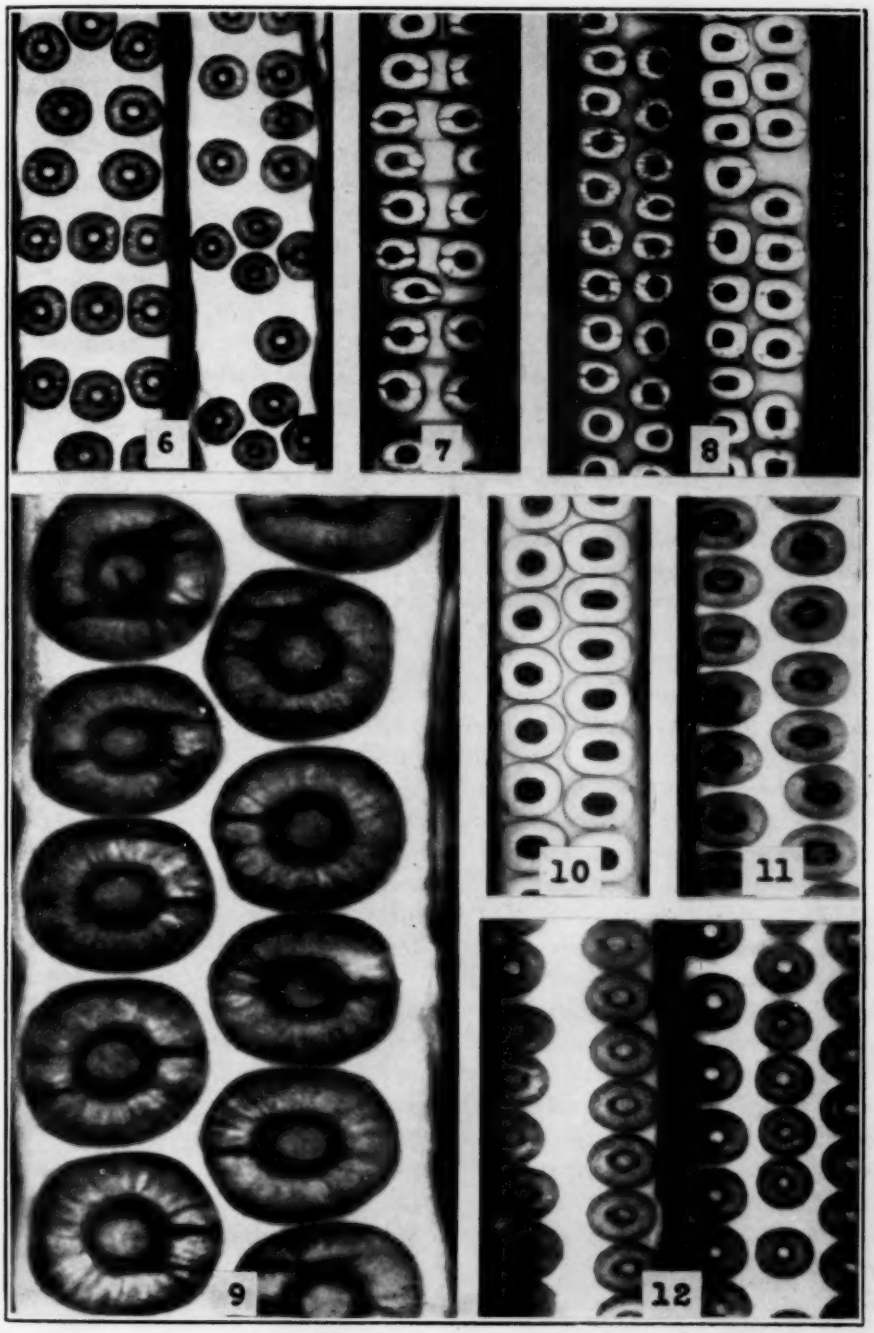
The bordered pits in the radial walls of tracheids in the secondary xylem of the native conifers are usually opposite, but as Thomson (1913) has shown in *Larix*, and Bailey (1933) has indicated for most of the other genera, an alternate arrangement is not uncommon. The latter is frequently to be seen in the first 20–30 growth rings in the distal parts of lateral roots of *Abies*, *Tsuga*, *Larix*, *Picea*, and less often in *Thuja* and *Pinus*. The more common opposite arrangement with conspicuous crassulae (rims of Sanio) is illustrated in figure 7, and without crassulae in figure 8. An alternating arrangement is shown in figures 8 and 9. Very wide tracheids often have three rows of pits, which may be grouped, opposite, or alternate, and crassulae may be present or absent (fig. 6). A similarly wide range of variation in arrangement of pitting and development of crassulae was observed in *Abies*, *Larix*, and *Picea* (figs. 10–12).

The alternating arrangement of pits occurred most frequently toward the overlapping ends of the tracheids where the pits were aggregated. It was found most often in the inner wood of lateral roots, seldom in the outer wood or in vertical roots. No outstanding generic distinctions in the proportion of alternate and opposite pits were noted between *Abies*, *Tsuga*, *Picea*, or *Larix*, but in *Thuja* and *Pinus* alternating arrangements were less numerous.

Some differences were observed in the torus and pit membrane. In *Abies* and *Tsuga* heavy bands extended across the membrane, usually in a radial direction from the rim to the torus (figs. 7, 8), but occasionally in a more or less tangential direction so as merely to come in contact with one side of the torus (fig. 9) or to avoid it completely. These bands gave the same staining reactions with ruthenium red and haematoxylin as the torus. They were not present in all pits, but generally were quite conspicuous in these two genera. They were seldom observed in *Larix*, *Picea* or *Pinus*. In the latter genera the margin of the torus is finely serrate (figs. 5, 10).

Explanation of figures 6–12.

Arrangements of pits on the radial walls of early-wood tracheids in the inner wood of the distal portions of lateral roots. FIG. 6. *Tsuga canadensis*. Grouped and opposite pits without crassulae. × 330. FIG. 7. *Tsuga canadensis*. Opposite pits with crassulae. × 330. FIG. 8. *Tsuga canadensis*. Alternate and opposite pits without crassulae. × 330. FIG. 9. *Tsuga canadensis*. Alternate pits, showing structure of the pit membrane. × 1300. FIG. 10. *Larix laricina*. Alternate pits. × 330. FIG. 11. *Larix laricina*. Alternate pits. × 330. FIG. 12. *Larix laricina*. Triseriate and alternate pits. × 330.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VERTICAL PARENCHYMA

Vertical parenchyma, apart from that associated with resin ducts, is common in the roots of *Tsuga*, usually abundant but sometimes infrequent in *Larix*, and generally scarce but occasionally abundant in *Picea*. The cells are terminal in distribution. A few parenchyma cells were observed in a root of *Pinus Banksiana*, but since they were seen in a transverse section cut from material which in the meantime had been discarded, there was no way of ascertaining whether they were separate xylem parenchyma cells or were simply the enclosing cells of a resin duct which had ceased a short distance above or below. In the Abietineae studied no definite trends in distribution were noted in different types of roots, or in roots from varied habitats, nor were any peculiarities in structure observed which might serve to distinguish such similar woods as *Picea* and *Larix*. In *Thuja* vertical parenchyma is common though variable in distribution. The cells are usually scattered throughout the growth rings, but sometimes, particularly when clearly associated with injuries, occur in tangential arrangement.

That xylem parenchyma is erratic also in stem wood, especially in the Abietineae, has been shown by Bailey (1909). The distribution and frequency of xylem parenchyma have been used for distinguishing fossil woods, but studies of living conifers show this character to be too variable to have any diagnostic value.

Unlike the separate xylem parenchyma, the parenchyma cells surrounding the resin ducts in the Abietineae vary both with the genus and the part of the tree. For instance, the epithelium lining the ducts in the wood of *Larix* and *Picea* is made up partly of thick- and partly of thin-walled cells, but there are usually more thin-walled cells in *Picea* than in *Larix*, and in both genera the proportion of thin-walled cells is higher in roots and in the outer wood of old stems than in the inner stem or branch wood (Bannan 1936). It may be noted here that the proportions of thin-walled cells, as given for roots in the paper cited, applied only to lateral roots. In vertical roots the percentage of thin-walled cells is somewhat lower than in lateral roots, but higher than in branch or stem wood of similar size and age.

The nature of the epithelium of resin ducts is of some diagnostic value when utilized in conjunction with other characters. However, in view of the variation between individuals and different parts of the tree, the epithelium alone should not be regarded as an infallible character for separating woods which closely resemble one another in other features, as for instance *Larix* and *Picea*.

THE DISTRIBUTION OF RESIN DUCTS

The total number of vertical resin ducts in the first 15 growth rings in 154 lateral roots of *Picea* (*P. glauca* and *P. mariana*) and *Larix* (*L. lari-*

cina) collected from various sites ranged from 15 to more than 200. Roots of the larch were obtained from two places near Toronto, and two sites on the north shore of Lake Superior. Very great differences in the average number of resin ducts were discovered in the roots from these sites (table 2). The fewest ducts were found in roots dug from muck in the bottom of a creek flowing through a black spruce and larch swamp in northern Ontario, and the greatest number in roots growing in a rather open swamp adjoining a field in southern Ontario. The abundance of ducts in the southern Ontario material may have been due to injury by grazing animals, for most of the land has been pastured at one time or another, and the lateral roots, located close to the surface, are liable to be injured. In black spruce also more ducts were found in the southern Ontario roots. A noteworthy feature of the northern Ontario material was that more vertical ducts occurred in the roots growing in gravel than in roots in uniform sand (table 2).

TABLE 2

Number of resin ducts in lateral roots

Species	Habitat	Av. ring width (mm.)	Av. total no. of vertical ducts in first 15 growth rings	Av. no. of horiz. ducts per sq. cm. at 3–5 mm. from pr. xylem
Larix laricina	Elevated silt-sand soil, S. Ont.	0.25	89	46
	Low ground, open swamp, S. Ont.	0.37	124	42
	Medium to coarse sand, dry sand plain, N. Ont.	0.35	66	31
	Muck, creek in swamp, N. Ont.	0.36	38	33
Picea mariana	Low ground, open swamp, S. Ont.	0.35	112	122
	Dry gravelly and stony soil, N. Ont.	0.24	93	83
	Medium to coarse sand, dry sand plain, N. Ont.	0.25	53	85
Picea glauca	Medium to coarse sand, dry sand plain, N. Ont.	0.40	76	84

The distribution of ducts in vertical roots was even more variable than in lateral roots. The most numerous ducts were observed in vertical roots (and in some oblique lateral roots) of *Picea mariana* extending down into gravelly and stony soils. These roots were decidedly eccentric and much distorted, and transverse sections revealed areas of cell disarrangement and open injury, especially in the outer growth rings. Apparently these injuries

were due to pressure exerted by the stones upon the enlarging roots wedged between them. Associated with the injuries were both extensive tangential series and scattered ducts (fig. 2).

Other vertical roots, particularly some of *Picea glauca* excavated from a medium to coarse sand without stones or other obstacles, had few ducts. The number in these was, on the average, only about half that observed in lateral roots growing on the same site, but closer to the surface of the ground. In fact, four of the vertical roots were almost lacking in ducts, the average total number in the first 15 rings being only 5, or an average of one duct every three rings. As is illustrated in figure 1, ducts were absent from large areas of the wood. The paucity of ducts was not attributable to lack of growth, since the rings were as wide as in roots with many ducts, but was evidently correlated with an absence of injury due to the nature of the medium in which the roots were growing.

The distribution of the horizontal ducts likewise varied greatly in different specimens. The horizontal ducts were more numerous in roots of both *Picea* and *Larix* collected in southern Ontario than in northern parts of the province, the distribution paralleling that of the vertical resin ducts in that respect (table 2).

The grand average number of horizontal ducts per sq. cm. of tangential section, determined at distances from 3 to 5 mm. from the primary xylem, was 84 in lateral roots of *Picea glauca*, 87 in *Picea mariana*, and 38 in *Larix laricina*. Similar numbers of horizontal ducts were observed in the outer rings, from 3 to 5 cm. from the center, in *Picea*, but in *Larix* the number in the outer rings was greater than in the wood nearer the center. Consequently the differences between the two genera observed in the inner wood tended to disappear in the outer rings. But even in the inner wood, where substantial differences were noted in the average values, the distribution was much too irregular to have any diagnostic value.

The roots of both larch and spruce are diarch as a rule, and in roots up to 1 cm. in diameter 20 per cent more horizontal ducts, on the average, were found in the radii parallel to the primary xylem plate than in the other sectors of the wood. Factors responsible for this increase were the origin of horizontal ducts from the primary, vertical ducts, and the greater numbers of rays in those radii.

The distribution of horizontal ducts in vertical roots (*Picea* spp.) was very erratic. They were numerous in some roots, particularly in those growing in gravel, and were scarce in others. In fact, in one root growing in a uniform sand the horizontal ducts were so rare as to be absent from tangential sections of considerable area. Vertical ducts also were very scarce in this root.

Since certain generic differences exist, the distribution of resin ducts

has been used as a character for differentiating the secondary xylems of living Abietineae and of fossils of Abietinean affinity. In *Abies, Tsuga,* and *Pseudolarix,* ducts, when present, are always of the vertical type and are arranged in tangential rows. Similar tangential series occur in *Cedrus,* but in this genus there are also horizontal ducts. In *Keteleeria* only vertically oriented ducts have been reported. These appear to be confined to tangential series in some specimens, and are distributed throughout the wood in others. Both vertical and horizontal ducts are found in *Picea, Larix,* and *Pseudotsuga.* The vertical ducts are usually scattered, but in some cases tangential series are also formed, and on rare occasions all the ducts are tangentially arranged. *Pinus,* likewise, has both vertical and horizontal ducts, but the former are generally dispersed throughout the wood and extensive tangential series very seldom occur in living species. The usual practice in the literature has been to describe tangential series of ducts as traumatic and a scattered pine-like distribution as normal. Evidence has been presented (Thomson and Sifton 1925; Bannan 1936) which indicates that the various Abietineae form a graded series and that the ducts, whether in tangential series or of the diffuse type, are correlated with extraordinary environmental circumstances. The distinction between traumatic and so-called normal ducts is based upon an erroneous conception of the character of the traumatic tissue in the pines and related forms.

Although the distribution of ducts in the Abietineae is usually that described above, variation in different specimens may at times be so great as to render this criterion unreliable. For instance, the secondary xylem of seedling stems, the inner wood of branches, and the wood of certain vertical roots of *Picea* may possess no ducts, ducts in tangential series, or a few scattered vertical ducts and only widely separated horizontal ducts. In some cases the wood is like that in *Tsuga,* or at times approaches the condition in *Keteleeria.* In contrast, other specimens may have numerous ducts with a pine-like distribution. Consequently, on the basis of the distribution of resin ducts alone, occasions arise when it is difficult to distinguish *Picea* wood from *Tsuga,* or in other cases from *Pinus.* Under such circumstances, the identification of woods whose sources are unknown must be made with the assistance of other characters, as for instance the nature of the epithelium surrounding the ducts, the structure of the rays, or other features of the primary or secondary wood.

A peculiar type of tissue, probably traumatic in origin, was observed in a root of *Picea mariana.* It occurred in three growth rings: the sixth, ninth, and fourteenth from the center. In each the tissue was found in small groups arranged tangentially, in contact with the late-wood tracheids of the preceding ring on one side, and surrounded on the other three sides by semicircles of thick-walled parenchyma cells (fig. 4). The tissue was com-

posed of thin-walled cells which stained deeply with haematoxylin but were unaffected by safranin. Since the outlines of bordered pits were discernible when the walls were viewed in radial sections, it is evident that the thin-walled cells were tracheids whose development had not proceeded much beyond the initial stages. Some resinous material was found in the areas. However, they differed from resin ducts in the absence of large intercellular spaces. In place of the extensive schizogenous cavities which characterize resin ducts there occurred incompletely developed tracheids.

HEIGHT AND DISTRIBUTION OF RAYS

The average height of the rays in the inner wood of the lateral roots of adult trees is shown in figure 15 for five species of native conifers. In all the height was calculated at points 3 mm. from the primary xylem, two determinations being made for diarch roots, one on the radius paralleling the primary xylem plate, and the other on the radius at right angles to the plate. The determinations were made along the roots at the distances from the stem indicated in the figure. Different trends in ray height were observed. In *Thuja* the rays were low in the distal as well as in the proximal parts of the roots, but in the other conifers the height was greater, and as shown in figure 15, increased sharply with distance from the stem. When comparison was made with branch wood it was found that the average ray height in the distal roots of *Thuja* was approximately the same as in branches of like size and age, whereas in *Tsuga* the rays were slightly higher in roots than in comparable branches, and in *Picea*, *Larix*, and *Pinus* were much higher than in branches.

In diarch roots 1 cm. or less in diameter, the average ray height varied on different radii, being generally somewhat greater on the radii at right angles to the primary xylem plate. The growth rings also were usually wider in those radii, but on the whole no correlation between ray height and ring width was observed in roots of this size. The height in roots with wide rings generally was no greater than in roots with narrow rings. In this respect the roots differed from stems or branches of similar size. In the latter the rays were higher in the specimens with the wider rings (Bannan 1937).

The average ray height in the outer wood of large lateral roots, several cm. in diameter, varied greatly. In some roots it was about the same as that in the inner wood. In others there was a slight increase, and in yet other roots, especially where the outer rings became sharply narrower, some of the ray rows ceased and the average ray height declined. Generally the rays were slightly higher in the outer wood on the upper than on the under side, but occasionally the reverse was true.

No consistent relationship was discovered between ray height and soil conditions. In *Picea mariana* the average height was somewhat greater in

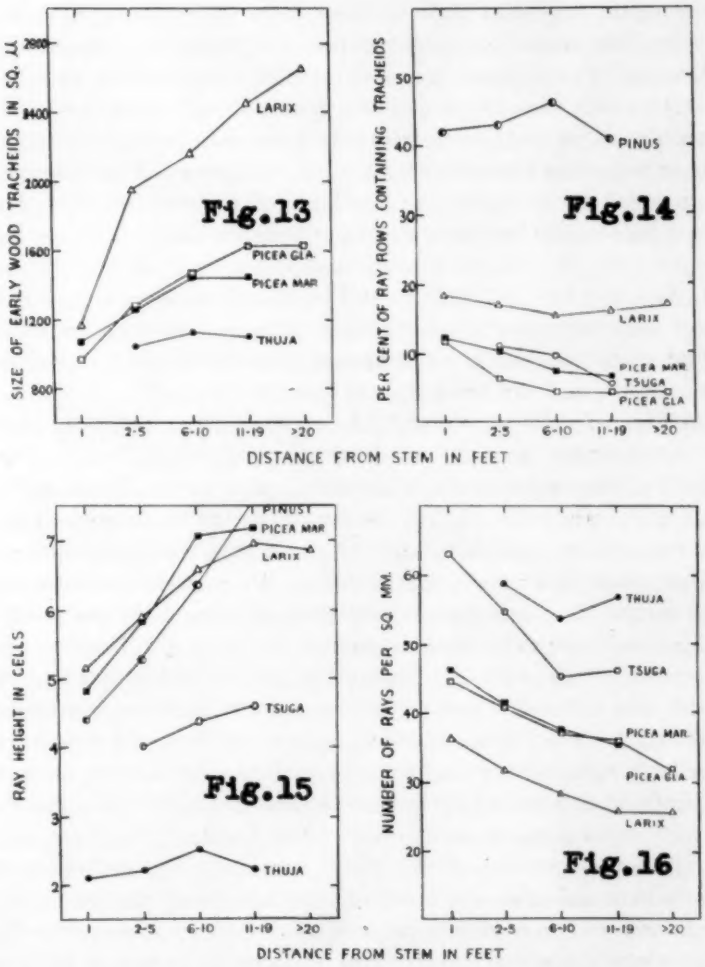

FIG. 13. Cross-sectional area of early-wood tracheids in lateral roots. The size of the tracheids was measured in the inner wood, 1 to 3 mm. from the primary xylem, and at the distances from the stem indicated. Data based on 174 sets of measurements. FIG. 14. Average percentage of ray rows containing ray tracheids in lateral roots. The percentage was determined at a distance of 3 mm. from the primary xylem; two calculations were made and averaged for diarch roots, one in the radial plane at right angles to the primary xylem plate, and the other in the plane paralleling the plate. Data based on 271 determinations. FIG. 15. Average ray height in lateral roots. The height was calculated at 3 mm. from the primary xylem, determinations being made from radial sections as described above. Data based on 295 determinations. FIG. 16. Average number of rays per sq. mm. of tangential section in lateral roots. The determinations were made at distances 3–5 mm. from the primary xylem. Data based on 263 calculations. The species are *Thuja occidentalis, Tsuga canadensis, Picea mariana, Picea glauca, Larix laricina,* and *Pinus Banksiana.*

roots growing in dry sand than in roots collected from swamps. A slight difference in the opposite direction was noted in *Larix laricina*, and in *Thuja occidentalis* and *Tsuga canadensis* no appreciable differences were observed between roots from these two types of habitat. These statements apply only to the smaller lateral roots, approximately 1 cm. in diameter. In larger roots of *Thuja occidentalis* the ray height in the outer wood was found to be greater in the drier habitats, but similar comparisons were not made for the other conifers. The range of variation between individuals on the same site was generally very much greater than the average differences between sites. At one site where a few roots of *Picea mariana* were collected from a very small area, the average ray height in one root was approximately double that in the others. The soil appeared to be uniform in texture and moisture content, and the trees were of similar size.

The number of rays per unit of tangential section, in lateral roots, was more or less inversely proportional to the ray height. In *Thuja*, where the rays were low, they were more numerous than in *Larix*, *Picea*, and *Pinus*, which had high rays (figs. 15, 16). Moreover in the latter genera the rays were less frequent in the distal parts of the lateral roots, where the height was greatest, than in the proximal portions. A factor in the lessening frequency of rays in the distal roots was the broadening of the tracheids which necessarily spread the rays farther apart.

The ray height in vertical roots (*Picea glauca*, *Pinus Strobus*, and *P. Banksiana*) was definitely lower than in lateral roots, and approximated the height in branches. The average height at 3 mm. from the primary xylem was 3.6 cells in *Picea glauca* and 3.8 cells in *Pinus Banksiana*, as compared with 5.5 and 5.3 cells in lateral roots the same distance from the stem. A like dissimilarity was noted in *Pinus Strobus*. Outward from the center of the roots the ray height increased slightly, but still remained below that in lateral roots. The average was 5 cells at 2–5 cm. from the primary xylem in vertical roots of *Picea glauca*, as compared with an average height of 6 to 7 cells in lateral roots of similar size, growing in the same kind of soil. In *Thuja occidentalis*, on the other hand, little difference was found between vertical and lateral roots, the average ray height being low in all roots.

Although different tendencies become apparent in various genera when a large amount of material is examined, both the height and distribution of rays vary too much from one specimen to another to be useful in differentiating closely related forms. For instance, the trends and average values in *Picea* and *Larix* are too similar to have any diagnostic value. Moreover the differences between individuals are much greater than the average differences between the two genera. The height and distribution of rays in *Thuja* differ markedly from the other conifers, but the wood of this genus may readily be separated from that of the Abietineae by other more reliable characters.

RAY STRUCTURE

The ray cells are principally parenchyma and tracheids, but the proportions of these cells differ greatly in various conifers. Ray tracheids were seldom found in the lateral roots of *Thuja*, they formed a small percentage of the ray tissue in the inner root wood of *Tsuga* and *Picea* (fig. 14), were more abundant in the roots of *Larix*, and made up from one-third to one-half the ray tissue in *Pinus*. In all genera ray tracheids were less numerous in lateral roots, particularly in the inner wood to a distance of 1 cm. from the primary xylem, than in stems or branches of similar size and age. The greatest difference between roots and stems was observed in *Picea glauca*, in which the proportion of ray rows containing ray tracheids was only 5 per cent in the inner wood of distal lateral roots as compared with from 20 to 40 per cent in stems; and the least difference in *Pinus* where ray tracheids were almost as abundant in some roots as in stems. The extent of these differences was indicated in a previous article (Bannan 1937), but it may be pointed out here that the values presented in that paper (table 1) for typical "buried" roots pertain to lateral roots only.

It is interesting to note that ray tracheids are usually slightly more numerous in stem wood of *Picea* (either *P. glauca* or *P. mariana*) than in *Larix* (*L. laricina*), but in roots the reverse is true. The proportion of ray tracheids in the inner wood of lateral roots of *Larix* was, on the average, twice that in *Picea* (fig. 14). In other words the degree of difference between root and stem was generally much greater in *Picea* than in *Larix*. This serves as another illustration of the manner in which conifers which closely resemble one another in many respects may differ markedly in the degree of reaction to similar environmental conditions in some other character. Relationships observed in one species are not necessarily of general application to the group as a whole.

Widely different proportions of ray tracheids were observed in the outer wood of the bigger lateral roots. In a large buttress root of *Picea Engelmanni*, examined at a point near the stem, ray tracheids made up 17 per cent of the ray tissue in the outermost rings on the upper side, but were absent on the under side. In another large lateral root, which was still 9 cm. in diameter at a distance of 12 feet from the stem, ray tracheids constituted less than 1 per cent of the ray tissue in the outer rings, both on the upper and under sides of the root. In other roots of *Picea Engelmanni* and in other species of *Picea* ray tracheids usually became more numerous in the outer rings. Thus in large lateral roots of *Picea glauca* and *P. mariana*, at distances from 1 to 10 feet from the stem, ray tracheids attained maximum values of from 20 to 30 per cent in the outer wood on the upper side, or nearly as much as in stem wood. In most roots ray tracheids were less numerous on the under side, the usual difference being from 5 to 10 per cent. Similar

proportions were observed in the outermost rings in large lateral roots of *Larix laricina*. In *Thuja occidentalis* the percentage of ray tracheids was very low throughout the wood in lateral roots, averaging 0.3 per cent at 3 mm. from the primary xylem and 1 per cent at 1–3 cm.

In *Larix* ray tracheids were most numerous in roots obtained from the northern parts of the province. The average proportions were 20 per cent in northern Ontario and 13 per cent in southern Ontario (the determinations being made at 3 mm. from the protoxylem in lateral roots at distances from 6 to 19 feet from the stem). In both regions ray tracheids were slightly more abundant in roots growing in swamps than in dry sand, but the average differences were so slight as probably to be without significance. Similar differences between roots in wet and dry sites were observed in *Picea mariana*. On the other hand no appreciable differences between roots in varied habitats were discovered in *Tsuga canadensis*, and in *Thuja occidentalis* ray tracheids were scarce in all roots.

Wide variations in number of ray tracheids were noted among certain individuals of the same species growing under apparently similar conditions. For instance, in one tree of *Picea mariana* the average per cent of ray tracheids in the inner wood of lateral roots was 17, in another 6. Several roots were examined, but the deviation from the average was relatively slight in each tree, the roots of one having a consistently high proportion of ray tracheids (11–22 per cent), and the roots of the other a low proportion (4–10 per cent). The trees were of like size and were growing in an open coniferous stand on a sand plain. Although it cannot be stated that the environment was identical for both trees, no appreciable differences were detected in soil texture, moisture, or root competition. It would seem that these particular variations in number of ray tracheids were due to genetic rather than to environmental factors. Certainly the differences between individuals in the same habitat were much greater than the average differences between those from such unlike habitats as dry sand plain and swamp.

The proportion of ray tracheids in vertical roots, as a rule, was no higher than in lateral roots, and in some was lower. In vertical roots of *Picea glauca* ray tracheids made up 7 per cent of the ray tissue 3 mm. from the protoxylem in both lateral and vertical roots, but 2–5 cm. from the center ray tracheids were usually less numerous in vertical than in lateral roots. In the material examined the proportions 2–5 cm. from the center were 14 per cent in vertical roots and 22 per cent in lateral roots. In *Pinus Banksiana*, *P. Strobus*, and the western *Tsuga heterophylla* and *Pinus ponderosa*, ray tracheids were slightly less numerous in vertical roots up to 1 cm. in diameter than in lateral roots of corresponding size. Larger vertical roots of these species were not examined. In all roots of *Thuja occidentalis* ray tracheids were scarce.

It is noteworthy that although vertical roots have wood which is stem-like in so many respects (tracheid caliber, extensive late wood, arrangement of pits in the walls of the tracheids, and height of the rays), the ray tracheids not only have not taken part in this development of a stem-like wood, but, in some roots at least, have deviated in the opposite direction.

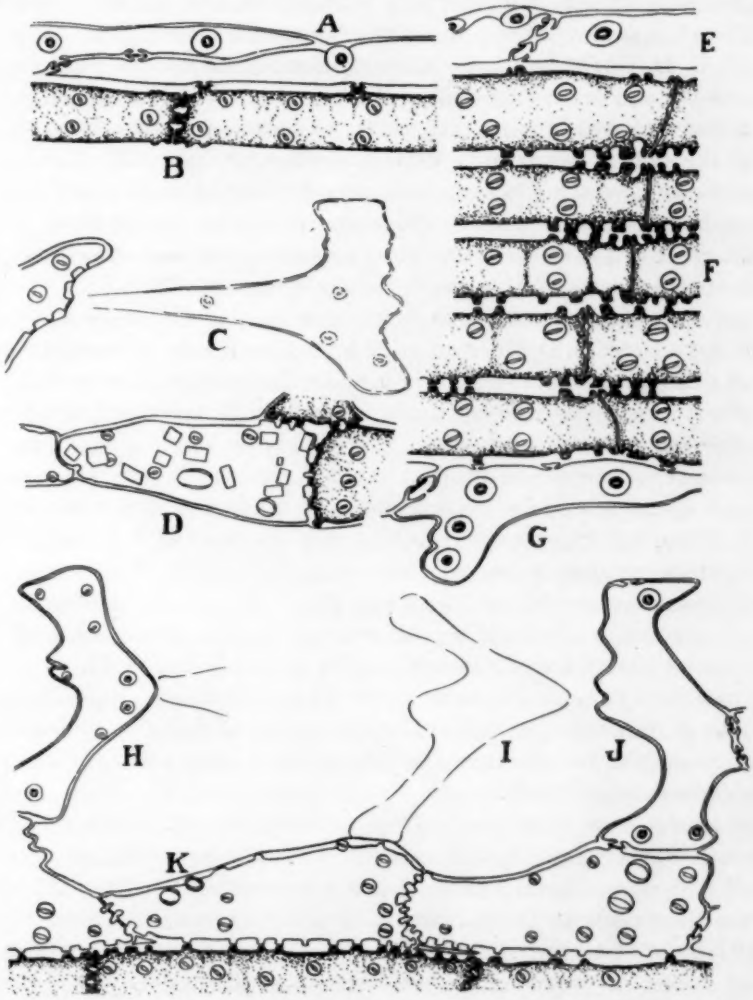

FIG. 17. *Larix laricina*. Types of ray cells in lateral roots. In the drawings of the parenchyma cells the pit apertures in the adjoining tracheids have been shown in addition to the margins of the simple pits in the walls of the ray parenchyma. Stippling represents protoplasm. Cells which are not stippled lack content, except in type D where crystals are present. Further descriptions in the text.

Ray tracheids were, in most of the specimens examined, slightly less numerous than in lateral roots of similar size, and were markedly less numerous than in comparable branch or stem wood.

In figure 17 are illustrated the different types of ray cells observed in the roots of *Larix laricina*. The ray parenchyma cells typically have thickened, lignified walls with simple pits. Between the pits are wall thickenings which sometimes have a knob-like appearance when viewed in radial sections (fig. 17, B, D, K). Occasionally these thickenings are much reduced, especially on the end or vertical walls (F). The protoplasm in the parenchyma cells usually persists for several years, but sometimes disintegrates early so that the cells appear empty (K) or contain crystals (D). The walls of the empty or crystal-containing cells may be very thin. The ray tracheids are devoid of protoplasm and have walls perforated by bordered pits (A and E). Some of the cells have vertical processes (G), and others, especially those near the origins of rays, are vertically elongated (H and J). The latter may have few pits, and these frequently are smaller (H) than in the more typical ray tracheids. Outlines of cells, known as ghosts, are occasionally to be seen near the points of ray origin or in the marginal rows of old rays (I). Sometimes the outline is a little more definite and small areas resembling pits can be recognized (C).

Although all the varied kinds of ray cell described above can sometimes be found in a single radial section, most of the ray cells are like types A and B. The other types occur rarely, but when present are usually to be found in new rays one or two cells high or in the marginal rows of the older, higher rays. The ray cells of *Tsuga* and *Picea* in general resemble those of *Larix*, though some minor differences were noted. For instance, the thinning of the end walls of ray parenchyma cells, shown in figure 17, F, was not observed in the roots of *Tsuga* or *Picea*. The ray cells of *Thuja* on the one hand and of *Pinus* on the other differ from those of *Larix* in some essential details which have been described or illustrated in other articles (Bailey and Faull 1933; Bannan 1934).

Certain features of the ray tissue are useful for differentiating coniferous woods. For instance, Bailey and Faull (1933) have demonstrated that the wall structure of the ray parenchyma cells distinguishes most Abietineae from the other conifers. Other features, however, such as the occurrence and proportions of the different types of ray cells are inconstant. Differences between genera or groups of genera observed in the majority of specimens, and which might accordingly be considered distinctive, sometimes disappear in other specimens or in certain parts of the tree.

On the basis of the ray cells in stem or branch wood the Abietineae may be divided into four rather ill-defined groups. In *Pseudolarix*, *Keteleeria*, and *Abies*, which may be considered as constituting one group, the rays are

made up of varied proportions of the following types of cells: ordinary ray parenchyma, parenchyma cells with typical wall structure but devoid of content, ghosts, and very thin-walled cells with or without crystals. In material examined by the writer the differences between these three genera appeared to be quantitative rather than qualitative. Ghosts and crystal-containing cells were least numerous in *Pseudolarix* and most frequent in some species of *Abies*, but differences between individuals, parts of the tree, and possibly between species, especially of *Abies*, were such that it seemed doubtful if the woods of these conifers could be positively distinguished by their rays. Ray tracheids occur rarely in *Abies* but are too sporadic to have any diagnostic value. *Cedrus* resembles the foregoing in the presence of ghosts and crystal-containing cells, but differs in the general occurrence of ray tracheids. *Tsuga*, *Larix*, *Picea*, and *Pseudotsuga* constitute a third group of Abietineae in which ray tracheids are generally numerous, and ghosts, thin-walled cells, and similar types are relatively rare. Here again, however, the proportions of ray tracheids and parenchyma cells vary so greatly that this feature of the ray tissue does not provide a means of differentiating the woods of these four genera. In the genus *Pinus* some species have rays resembling those in *Picea*, while in other species ray tracheids are more numerous, the walls are further elaborated, and the ray parenchyma cells are also different.

The differences described above for stem or branch wood do not necessarily apply to root wood. For example, ray tracheids, although abundant in mature stem wood of *Picea*, are sometimes lacking in root wood. The problem of identification of the fossil woods is further complicated by the fact that the proportions of the various types of ray cells sometimes differed materially from those obtaining in their nearest living relatives. Ray tracheids are unreported in most fossil gymnosperm woods. These cells were observed by Arnold (1930) in certain species of *Callixylon*, and some tracheary cells of peculiar type have been described by Andrews (1940) for *Lyginopteris*, but generally the rays seemed to have been parenchymatous. Even in some of the Cretaceous pines ray tracheids occurred rarely or were lacking. These cells were not found in *Pityoxylon foliosum* and *P. anomalum* (Holden 1913), or in *Pityoxylon statenense* and *P. scituatense* (Jeffrey and Chrysler 1906). In *Pityoxylon scituatensiformis* (Bailey 1911) ray tracheids did not appear in the first 10–15 years' growth and were poorly developed in the subsequent wood.

In some fossil woods cells have been observed which, it was said, resembled or suggested ray tracheids but could not be positively identified as such. These indefinite cells have been reported in *Protopiceoxylon* by Seward (1919) and Read (1932). Stopes (1915) has illustrated for *Pityoxylon Benstedi* and *P. Sewardi* ray cells with simple pits in one wall and what were

described as bordered pits in other walls. These cells were considered to be ray tracheids, but if cells have such mixtures of pits they obviously are not typical ray tracheids. Holden (1913), describing a Cretaceous *Pityoxylon*, noted cells along the margins of rays which were irregular in shape and destitute of resinous content. She stated that at first sight these cells appeared to be ray tracheids, but was careful to point out that the unbordered character of the pits negatived that possibility.

Irregular outlines, lack of content, and marginal position in the ray do not suffice to identify cells as ray tracheids. These characters are also common to certain parenchyma, thin-walled cells, ghosts, and other types which occur in varying proportions in the secondary xylem of living Abietineae. Only the presence of bordered pits exclusively can be considered an infallible criterion for establishing cells as ray tracheids. In radial sections this involves distinguishing between half-bordered pit-pairs, such as occur between tracheids and ray parenchyma cells in most Abietineae, and the full-bordered pit-pairs found between tracheids and ray tracheids. Since empty, irregularly shaped parenchyma cells, thin-walled cells, and other types occur in large numbers in certain living Abietineae, and are present to some degree in most genera, their occurrence is to be expected in fossils of Abietinean affinity. Possibly some of the indefinite cells reported in the literature are of these types.

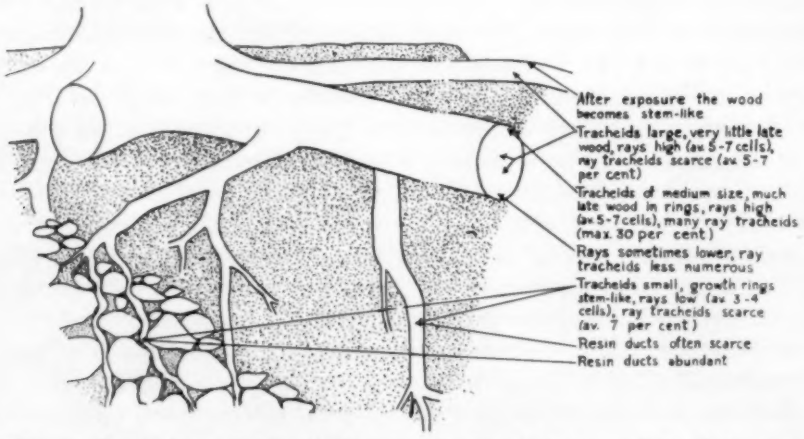
After exposure the wood becomes stem-like
Tracheids large, very little late wood, rays high (av. 5-7 cells), ray tracheids scarce (av. 5-7 per cent)
Tracheids of medium size, much late wood in rings, rays high (av. 5-7 cells), many ray tracheids (max. 30 per cent)
Rays sometimes lower, ray tracheids less numerous
Tracheids small, growth rings stem-like, rays low (av. 3-4 cells), ray tracheids scarce (av. 7 per cent)
Resin ducts often scarce
Resin ducts abundant

FIG. 18. *Picea glauca*. Schematic diagram of roots to show correlation between wood structure and location in the root system.

SUMMARY

A study was made of the secondary xylem in roots of native conifers to determine the range of structural variability within the species. Material was collected from varied habitats and from different parts of the root sys-

tems. The conifers investigated were the local species of *Thuja*, *Tsuga*, *Abies*, *Larix*, *Picea*, and *Pinus*.

A fine-textured, stem-like wood was found in the roots of small trees, in the upper side of buttress roots of mature trees, about the periphery of the largest lateral roots, in roots exposed by soil erosion, and in vertical roots deep in the soil. An open wood with large early-wood tracheids and little development of late wood was observed in the first one or two centimeters of growth in the distal parts of lateral roots located in the top few inches of soil (see fig. 18).

The diameter of the tracheids varied greatly in different parts of the root system, the greatest range being noted in *Larix*, the least in *Thuja*. No consistent relationship was discovered between tracheid size and soil moisture.

The pitting in the radial walls of the tracheids varied from opposite to alternate, the latter arrangement occurring most frequently in the inner wood of lateral roots of *Tsuga*, *Larix*, and *Picea*. Alternate pits were less abundant in *Thuja* and *Pinus*.

Vertical parenchyma cells were of erratic distribution in most of the genera studied. No trends were observed in different parts of the root systems.

The distribution of resin ducts was exceedingly variable. Ducts were most numerous in injured material, fewest in apparently unharmed specimens, for instance certain vertical roots penetrating deep into uniform sand. In such roots (*Picea glauca*, fig. 18) resin ducts were usually scarce, large areas of the wood possessing neither vertical nor horizontal ducts.

The height and distribution of rays varied greatly, both in different parts of the root systems and in different conifers. In general, the rays were highest and least numerous in the distal parts of lateral roots and lowest in vertical roots. The range of variation within the root system of a single tree was greatest in certain Abietineae, least in *Thuja*.

The proportions of the various kinds of ray cells (tracheids, parenchyma, and other types) varied throughout the root system and from one genus to another. The greatest variability was observed in *Picea* and the least in *Thuja*.

Because of this great variability in wood structure it is clear that anatomical studies must be based upon wide selections of material if they are to have taxonomic value.

The writer wishes to express his thanks to Professor R. B. Thomson for his interest in the work, and to Dr. D. H. Hamly for generous assistance with the photomicrographs.

Department of Botany, University of Toronto
Toronto, Ontario

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RAPID IDENTIFICATION OF THE MONTANE–SUBALPINE ZONE BOUNDARY[1]

RONALD L. IVES

(WITH ONE FIGURE)

In various parts of the Rocky Mountains, extreme difficulty has been experienced in making rapid, but reasonably accurate, differentiation between the montane and subalpine vegetative zones, which, in these areas, intergrade like the various minerals in a complex isomorphous series. This difficulty is further increased by the extreme irregularity of the zone of transition, a result of great local variations in water supply, temperature, soil, and effective solar radiation.

Where topographic relief is from slight to moderate, and soil and climatic conditions are reasonably uniform, zonal boundaries may be determined at a very few points, with any accuracy desired, and these findings extrapolated for considerable distances without introducing appreciable errors. Zonal definitions based solely on altitude are reasonably accurate in such areas.

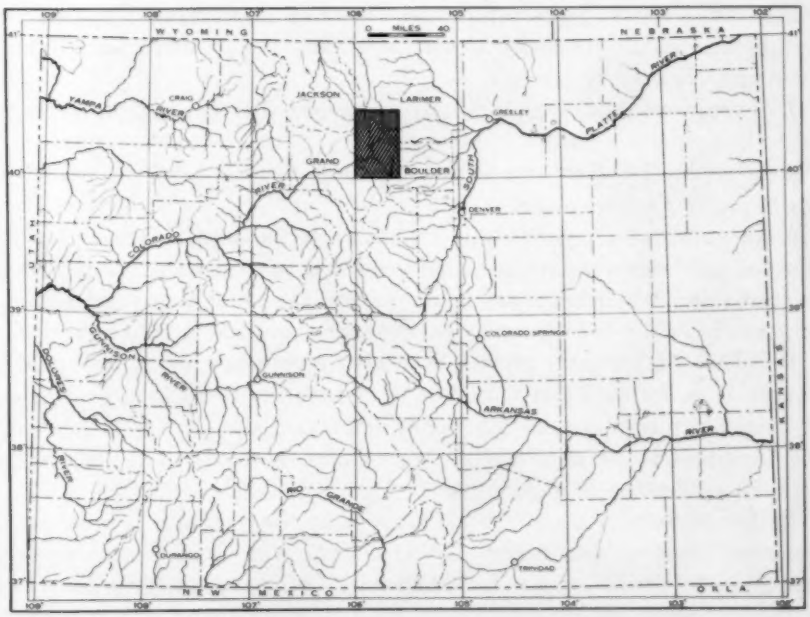

FIG. 1. Outline map of Colorado. Area of principal studies shaded.

[1] Research assisted by grants from the Penrose Fund of the American Philosophical Society.

Altitude ranges of the various life zones in Rocky Mountain National Park, Colorado, are stated by Ashton (1, pp. 6–13).

Studies in the upper valley of the Colorado River (fig. 1), and in adjacent parts of the Front and Never-Summer Ranges, showed that extrapolations of more than a few thousand feet were hopelessly inaccurate in many areas. Complicating the biotic relations in this structurally and stratigraphically complex region are extreme local variations in climate, due in part at least to topographically-controlled convections (2) in the deep valleys carved into the mountain flanks during repeated Pleistocene glaciations.

Studies of plant successions in this area disclose that wherever montane forest cover has been removed, whether by lumbering, fire, avalanche or solifluction, the replacement growth is aspen (*Populus tremuloides*); and that where subalpine forest has been destroyed, replacement growth is limber pine (*Pinus flexilis*) in windswept areas, and predominantly lodgepole pine (*Pinus contorta*) where shelter is adequate. Montane and subalpine replacement growths tend to be mutually exclusive during the first few decades of reforestation, so that the dividing "line" between zones is relatively sharp.

Field investigations show that the transition from aspen to evergreen, as replacement growth, falls within the "zone of uncertainty" between the montane and subalpine zones. From these data, the following zone-identification criteria may be stated:

1. If replacement growth is wholly evergreen, the area is in the subalpine zone.

2. If replacement growth is predominantly aspen (80% or more), the area is in the montane zone.

3. In an area of considerable relief, where natural reforestation is in progress, and where the replacement growth is predominantly aspen at low elevations and wholly evergreen higher up, the transition from aspen to evergreen indicates the boundary between montane and subalpine forest.

4. Where replacement growth is mixed, with aspen not predominating, the area is in the montane zone, but the upper limit of aspen growth does not necessarily indicate the interzonal boundary, and may be far below it. This condition is common where reforestation is approaching completion, or where solifluction is in progress.

Rather obviously, these criteria may be applied rapidly, for aspen and evergreen growths are easily distinguished, even at a distance, either visually, or by use of infra-red photography (3). Areas undergoing reforestation can usually be identified without difficulty. Growths that are undeniably of the replacement type can be found in avalanche scars, which are most numerous on valley walls in the very localities where it is most difficult to distinguish between montane and subalpine forest by the usual methods,

and where extrapolations from a few carefully-determined points tend to be least accurate.

These criteria appear sufficiently accurate for use in all but highly detailed studies in the Colorado Front Range area between latitudes 39° and 41°, and seem applicable southward to at least latitude 36°, as indicated by rough reconnaissances. Although they will probably be useful in many other parts of North America, either as stated, or with slight modifications, these criteria should not be depended upon, at any great distance from the Colorado Headwaters area, until they have been carefully checked, and their validity, for the area under consideration, definitely shown.

BOULDER, COLORADO

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CONTRIBUTIONS TO THE BIOLOGY OF POLYPORUS RHEADES (PERS.) FRIES

H. E. Bailey

(WITH TWO FIGURES)

Polyporus rheades (Pers.) Fries is a common fungus in California, causing a destructive white-piped rot of oak.[1] The fungus is particularly common in the vicinity of Mount Diablo, Contra Costa County, California, where sporophores were found on several species of oak. *Quercus Wislizenii* A. DC., *Quercus lobata* Neé, and *Quercus Douglasii* H. & A. were those most severely attacked. Cross sections through the trunks showed most of those which were from three to four feet in diameter badly decayed, as well as many of the smaller ones (fig. 1).

FIG. 1. Cross and longitudinal sections of a portion of a rotted trunk of *Quercus agrifolia* showing the typical mottled rot caused by *Polyporus Rheades*.

Sporophore formation occurs during the fall, usually between the months of September and November. The scarcity of sporophores at other seasons of the year may perhaps be explained by the fact that they are early attacked by insects. In the Mount Diablo region the fruiting bodies are disin-

[1] Hedgecock, G. G., and Long, W. H., Heart-rot of Oak caused by *Polyporus dryophilus* Berk. Jour. Agr. Res. 3: 65–80. 1914.

tegrated by a particular insect, *Tinea defectella* Zell., the larvae of which bore through the sporophore and honeycomb it with channels.

Sporulation in nature may be very abundant. In one instance it was noted that a deposit of spores 3–4 millimeters thick had collected under a sporophore which had grown in such a manner as to form a protective pocket between the pore surface of the sporophore and the bark of the tree. Freshly collected sporophores brought into the laboratory were very sensitive to changes in orientation and, in spite of precautions taken during transit from the field to the laboratory, the pore surface soon became covered with a new growth of mycelium. Shallow pores occasionally developed when these sporophores were kept under a bell jar, but sporulation never occurred from the newly formed pores. Sporophores produced in culture cast spores abundantly, some for a period of 30 days. The spores shed during this period in one culture weighed over 100 mg. (air dry weight).

Germination of the spores was erratic and the percentage low. Spores obtained from spore traps, spores shed directly onto the agar substratum, and spores produced from sporophores in culture were used in the germination tests. No germination occurred when the following substrata were used: plain 2 per cent agar, corn meal agar, malt extract agar, agar with 1 per cent phosphoric acid, or 1 per cent lactic acid, Leonian's agar, and oak agar. Spore germination was obtained, however, in a malt extract medium in which the mycelium had previously been growing. Drops of the filtered, sterilized medium were placed upon the lid of a Petri dish with sterile water in the bottom to keep the humidity high. These drops were then inoculated from a spore suspension. Examination showed about 15 per cent of the spores germinated.

In order to study the changes occurring in wood during the processes of decay, chemical analyses were made of samples taken from wood blocks which had been exposed to the fungus and which had lost 22.5 per cent, 29.7 per cent and 44.7 per cent in weight during successively longer periods of exposure to the fungus. The wood blocks were prepared as follows: a seasoned section of trunk of *Quercus agrifolia* nine inches in diameter was sawed into pieces one inch square and three inches long. These were soaked in water for one hour at reduced air pressure and then sterilized in an Arnold steam sterilizer on three successive days for a period of a half hour each. The blocks were then removed from the containers and placed on glass slides in previously prepared culture dishes in which a heavy mat of mycelium had been allowed to develop. In the preparation of these dishes a 2 per cent malt extract agar was inoculated with sporophore tissue.

The culture dishes containing the blocks of wood were kept in a humid chamber at 25° C. Color changes caused by the action of the fungus on the wood were early noticeable. The wood became progressively lighter in color

and, in the most advanced stages, had a bleached appearance, with thin, dark, zone lines running irregularly through it (fig. 2). The rotted wood

FIG. 2. Sporophore of *Polyporus Rheades* developed on wood block in culture. The dark zone lines in the wood are characteristic.

appeared stringy, was soft and spongy, and could easily be torn apart with the fingers.

Samples of decaying wood were taken at various intervals during the exposure to the fungus, their loss in weight determined, and the components analyzed and compared with those of sound wood (table 1). Analyses were

TABLE 1

Chemical analysis of sound and decayed wood of Quercus agrifolia and tissue of Polyporus Rheades.

	Wood decayed in culture			Sound wood	Wood decayed in nature	Mycelium	Sporophore context
Loss in weight	22.5%	29.74%	44.7%		54.9%		
H_2O Sol.	9.22	9.09	6.77	15.65	4.33	17.52	13.85
Alc. Ben. Sol.	1.39	1.29	1.04	4.81	1.62	9.69	3.45
Cellulose	50.37	42.15	35.28	52.3	24.48	69.0	39.8
Lignin	10.81	6.46	6.90	20.8	15.42	55.0	60.8
Pentosans	15.50	14.50	12.0	22.6	7.53	2.37	0.777
Ash	0.868	0.95	1.12	2.34	0.889	0.945	0.217

also made of fungous tissue both from sporophores obtained in the field and from mycelium grown on wood blocks. Comparing the utilization of wood components by the fungus, we see that there is a progressively greater utilization of each of these in samples taken at successive intervals. The values obtained for the sporophore context and the mycelium differ appreciably from those obtained for wood.

BERKELEY
CALIFORNIA

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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